Factors Influencing Riparian Breeding Bird Communities along the Middle and Lower Yellowstone River

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EXECUTIVE SUMMARY

Riparian zones constitute a very small portion of the landscape, yet they provide some of the most diverse and productive habitats for native birds in the western US. However, most river systems in the US have been subject to intensive water management and human development, and the extent and condition of their riparian habitats have been degraded. Consequently, those rivers that still support extensive native riparian plant communities are especially important to riparian birds. The Yellowstone River in Montana is one of the few remaining free-flowing rivers in the lower 48 states, and supports heterogeneous riparian plant communities which provide habitat for many native bird species. Relatively intact riparian systems, such as the Yellowstone River, may serve as a reference for understanding the factors that influence the distribution of birds along the length of a river, and provide valuable information for the management of rivers and native wildlife species. In 1999, the Yellowstone River Conservation District Council was formed to address concerns about the cumulative effects of human activities along the middle and lower stretches of the Yellowstone River. This study was designed to examine the relationships between birds and environmental factors within the riparian corridor of the Yellowstone River. Knowledge about relationships between birds and characteristics of the environment will provide a better understanding of the potential impacts of land and water management decisions that might modify the availability of particular resources within the riparian zone. Given that the same environmental factors often influence the distribution and abundance of many different types of terrestrial wildlife species, this information will also allow for a general assessment of the potential influences of management on other native riparian species.

We investigated the factors influencing community characteristics and the distribution and abundance of breeding birds along a 725 kilometer (450 mile) section of the Yellowstone River in central and eastern Montana. Birds and vegetation were surveyed within riparian habitats along braided sections of the river in order to describe patterns of bird species richness, bird occurrence, and bird abundance, and to examine the factors influencing bird distribution. Objectives were to:

1) Identify important factors influencing riparian bird communities, including characteristics of local habitat, forest cover, and land use;
2) Describe how characteristics of habitat, forest cover, and land use are distributed along the length of the river;
3) Assess the influences of habitat, forest cover, and land use on bird community characteristics and the distribution and abundance of particular species;
4) Quantify the additional effects of river location on birds, after accounting for the effects of habitat, forest cover, and land use; and
5) Examine the potential influences of Russian olive on bird species richness and abundance

Birds were sampled in 2006 and 2007 using point count methods at 304 randomly chosen sites in 21 braided or anabranching reaches along the river. Sixty-four species of birds were recorded over the two years. Bird communities were surveyed only in braided and anabranching reaches because the most extensive stands of riparian vegetation are located within these reaches and because multi-channel reaches of the river are likely to be most impacted by any future river management activities. Each site was visited multiple times within a season, and sites were visited in both years. Birds were sampled in grassland, shrubland, and cottonwood forest habitats. Most study sites were located in mature cottonwood forests because cottonwood forests support the most diverse plant and breeding bird communities of all riparian habitats, and because we wanted to ensure that adequate samples could be attained in all types of cottonwood forest habitat. Surveys were conducted in eight counties (Carbon, Dawson, Richland, Rosebud, Stillwater, Sweet Grass, Treasure, and Yellowstone) on the lands of 60 private landowners, and thirteen parcels of public land.

Vegetation data were also collected at these sites to quantify local habitat characteristics, and were used to identify the habitat type for each site surveyed. Aerial photographs were used to quantify forest cover and land use. Variables representing these factors included: the percent forest cover within 200 meters of each survey site, the distance to the nearest crop field, and the distance to the nearest human settlement. River kilometer was used to quantify the location of a site along the length of the river.

Multiple measures of bird community characteristics were examined: Total bird species richness (the number of bird species observed at each site), richness of Neotropical Migrant (NTM) species, and richness of species in various foraging and nesting guilds. NTM species winter south of the US in Central and South America and were included in analysis because they are of specific conservation and management concern. A 'guild' is an association of species that use resources in a similar way. Analysis of nesting and foraging guild richness may provide additional information about the types of species that are using different habitat types. The influence of environmental variables was also examined for fourteen individual species of birds.

A diversity of local habitats existed within the floodplain of the Yellowstone River. Three broad habitat types were identified: mature cottonwood forest, shrubland, and grassland. Cottonwood forest sites were further divided into five habitat types that encompassed a gradient of changing canopy and understory conditions, ranging from cottonwood forest with an open canopy and few trees and shrubs, to forest with higher canopy cover and a dense understory of native shrubs. Structural differences in vegetation characteristics were evident between habitat types. The abundance of small and large diameter trees, small and large native shrubs, Russian olive stems, and percent canopy cover all differed to some degree between habitat classes.

Local habitat characteristics were important drivers of bird distribution and abundance. Species richness varied across cottonwood habitats, and was highest in the two habitats that had the highest densities of native shrubs in the understory. Patterns of richness of NTM species were very similar to total species richness. Guild richness also differed across cottonwood habitats for many of the foraging and nesting guilds. Cottonwood habitats with native shrubs in the understory supported higher numbers of species that foraged in shrubs, and nested on the ground and in shrubs. Richness of species that forage on the ground was lowest in the habitat with densest canopy cover, a relatively open understory, and the highest density of Russian olive; however, more species that forage in the canopy were found in this habitat. These results suggest that different habitats provide different types of resources for birds. Habitat preferences tended to reflect the niche requirements of each species. A variety of species were observed breeding within cottonwood forest habitats, ranging from species that nest and forage in the canopy, to those that nest and forage on the ground. Most of the 14 individual species exhibited a positive or negative association with at least one cottonwood habitat type, indicating that different species were using different habitat types. All of these results suggest that the existence of a variety of habitat types within the floodplain is a major factor contributing to the diversity of bird communities within the riparian zone.

Forest cover was an important factor influencing abundance or distribution for most of the species. Although riparian forests are generally patchy in nature, forest cover within cottonwood habitats along the Yellowstone River ranged from sparse to relatively dense, and this range in forest cover was present along the length of the study area. Consequently, riparian habitats supported bird species that prefer edge habitats as well as species that are associated with more contiguous forest tracts. This suggests that the existence of a variety of forest cover conditions within the floodplain is important for maintaining populations of riparian breeding bird species (especially those species that are dependent upon dense forest cover and large forest tracts) and overall bird diversity.

Many species also exhibited a significant response to the proximity of agriculture and human settlement to the riparian zone. For most of the species that were influenced by the proximity of crop fields, higher occupancy or abundance was observed at sites where crop fields were close to the riparian zone. These species were all edge habitat species, suggesting that crop fields may provide an abrupt edge that is otherwise not common in patchy cottonwood forests. Proximity to agricultural fields has previously been shown to reduce nest productivity by introducing exotic or pest predator species into riparian habitats. However, we collected only presence/absence data for this study, and were not able to quantify the effects of agriculture on the productivity of bird populations.

Human settlement was highest in the western region of the study area near the foothills of the mountains, and declined steadily toward the mouth of the river. A few bird species were significantly affected by the proximity of human settlement to the riparian zone. The brown-headed cowbird was one species that was positively associated with human settlement. Cowbirds lay their eggs in the nests of other songbird species, and have been implicated in the population declines of many species of riparian birds. The potential effects of land use on bird populations have direct management implications when considering the consequences of increased land use in the floodplain. However, the influences of land use on bird abundance and distribution are also manifested indirectly, because increased agricultural production or human settlement within the floodplain may cause an increase in bank stabilization or water management in an effort to reduce the loss of property from flooding or erosion. These management activities may result in a degradation or loss of important riparian habitats for birds.

Even after accounting for the effects of local habitat, forest cover, and land use, river location was one of the most important factors influencing the abundance and distribution of bird species. Most of the relationships with river location were either negative or positive (i.e. higher abundance or occupancy at one end of the study area or the other). Bird response to river location may reflect important unmeasured environmental conditions that change along the downstream gradient, but are difficult to quantify (e.g. abundance of insect food resources). Alternatively, variation in distribution or abundance may reflect broader scale non-environmental influences, such as the geographic range of a species within a region or continent. The influence of river location on riparian birds presents a challenge when considering the effects of management over a large area, such as the length of a major river system, because traditional factors that are often used to measure habitat quality (i.e. local habitat, forest cover, and land use), may not adequately explain the observed variation in characteristics of bird communities. Therefore, it may be necessary to also consider relationships with geographical location when attempting to understand the potential consequences of management for bird communities within the river system as a whole. For example, management activities may need to be considered within the context of particular reaches or ecoregions of the river, as different bird communities may be present within a given habitat type that exists in reaches or ecoregions along the length of the river.

There was no evidence that species richness was affected by the abundance of Russian olive. Significant relationships were observed between Russian olive abundance and bird abundance, but the effect of Russian olive was similar to the effect of tall native shrubs, suggesting that birds may be responding to habitat structure in general and not Russian olive in particular. It is difficult to understand how the abundance of Russian olive influences bird communities using only presence/absence bird data collected at randomly located sites. Previous studies have reported that bird species richness and abundance are higher in native forest, likely due to higher insect abundances found there. If Russian olive is excluding native shrub species in the understory of cottonwood forests, then bird species richness and abundance may decline due to the further expansion of Russian olive trees into the riparian zone. This may be especially relevant to bird communities along the Yellowstone River because highest bird species richness was observed in cottonwood forest habitats with native shrub in the understory. Further studies that are specifically designed to investigate the influence of Russian olive compared with native habitats are necessary to understand the real implications of its expansion into the riparian zone along the Yellowstone River.

Few studies exist that document characteristics of bird communities along the length of a major river system, because it is difficult to systematically survey birds over large geographic areas, and it is often logistically complicated to gain access to private lands within riparian zones. Consequently, the information gathered in this study will provide valuable insight about the distribution of birds not only along the Yellowstone River, but also within the floodplains of major river systems in general. Few data exist that document the historical distribution of bird species within the riparian zone of the Yellowstone River, so it is impossible to quantify the status of bird communities today relative to the past. However, in this study we demonstrated that the riparian corridor provides breeding habitats and resources for many different types of native bird species. The knowledge acquired in this study will provide a more comprehensive understanding of the potential influences of floodplain management on riparian species, and allow for an assessment of the consequences of management for all wildlife that are dependent upon the unique habitats and resources provided by the Yellowstone River.

INTRODUCTION

The value of riparian zones to native bird species is well understood (Kauffman et al. 2001), particularly in the semi-arid regions of the western United States where mesic, productive riparian lowlands provide an abundance and variety of habitats and food resources that are not found in the uplands (Austin 1970, Stauffer and Best 1980, Szaro 1991, Lehmkuhl et al. 2007). Much of the heterogeneity within the riparian zone is due to complex geomorphology and regular flood disturbance; floods initiate succession by eroding away plants and sediment, and redepositing alluvial material downstream to create bare sites for the establishment of new vegetation. Many riparian plant species have evolved to establish and persist in flood-disturbed areas, and depend upon flood disturbance for regeneration. However, river management activities, such as the construction of dams or stabilization of braided channels, may alter geomorphology, hydrology, and the frequency and intensity of disturbance which consequently limit erosion, river channel migration, and overbank flooding (Hupp and Osterkamp 1996). These control measures reduce flood disturbance and inhibit the regeneration of riparian vegetation, leading to substantial changes in the extent, distribution, and structure of riparian habitats available to native bird species.

To understand the consequences of environmental changes that result from management activities within the floodplain, it is essential to identify the factors influencing the distribution and abundance of riparian bird species. Many studies have examined the effects of local habitat characteristics, such as vegetation structure and composition (Miller et al. 2004, Strong and Bock 1990, Farley et al. 1994, Fleishman et al. 2003), site-level habitat, such as the extent of riparian forest cover in the surrounding landscape (Hodges and Krementz 1996, Kinley and Newhouse 1997, Whitaker and Montevecchi 1999, Hagar 1999, Groom and Grub 2002, Perkins et al. 2003), and adjacent land use (Tewksbury et al. 1998, Tewksbury et al. 2006, Hennings and Edge 2003, Saab 1999) on the distribution, abundance, survival, and productivity of riparian birds. Most of this information has been collected within a particular reach or small region of a river system (but see Saab 1999). However, the floodplain of a river system is often heterogeneous, with general downstream changes in environmental conditions as a river flows from its headwaters to its mouth (Malanson 1993, Schlosser 1987, Vannote et al. 1980, Benke 2001, Brinson 1993). Therefore, a broad-scale examination of riparian bird communities is necessary to provide complete information about the factors influencing the distribution of birds within a river system as a whole.

Besides local habitat, surrounding forest cover, and land use, there are certain environmental conditions that may change along the downstream gradient that are difficult to quantify, yet important to birds. For example, aquatic and floodplain invertebrates, which are an important food source to riparian insectivorous birds, may change predictably along the length of a river in response to changing hydrology and flood dynamics (Vannote et al. 1980, Reese and Batzer 2007, Arscott et al. 2005). Assessment of the relationships between geographic location along the river and bird distribution, while simultaneously examining the influences of habitat, forest cover, and land use, may provide insight into the importance of unmeasured environmental factors. Geographic location may also represent non-environmental factors that influence the range of a species, such as regional population dynamics or the influences of historical patterns of colonization and extinction (Hanski 1999, Storch et al. 2003). When examining the factors affecting the distribution of birds over broad scales, such as along the length of a major river system, relationships with geographical location may provide evidence for the influence of factors not directly related to environmental variables.

Knowledge about the factors influencing the distribution of birds within the floodplain of a river system can provide a comprehensive understanding of the potential influences of floodplain management on riparian birds. Information collected at broad-scales is especially relevant for rivers and riparian zones, given that the impacts of management activities are not restricted to the local areas where they are implemented. Instead, they often extend downstream and throughout the floodplain through changes to hydrology, sediment loads, and the frequency and intensity of flood disturbance.

Most river systems in the US have been subject to intensive water and channel management. Those rivers that still experience historical flood cycles and support extensive native riparian plant communities are especially important to riparian birds. The Yellowstone River in Montana is one of the few remaining free-flowing rivers in the lower 48 states, supporting extensive, heterogeneous riparian plant communities which provide habitat for many native bird species. Relatively intact riparian systems, such as the Yellowstone River, may serve as a reference for understanding the factors that influence the distribution of birds along the length of a river, and provide valuable information for the management of rivers and native wildlife species.

Major flooding in 1996 and 1997 along the Yellowstone River lead to increased public concern about the impacts of human activities along the river, particularly bank stabilization, development within the floodplain, and invasive species. These events highlighted the need to collect and compile scientific data along the entire length of the river to be used for informing management decisions. In 1999, the Yellowstone River Conservation District Council (YRCDC) was formed to address concerns about the cumulative effects of human activities along the middle and lower stretches of the river, and Congress authorized the US Army Corps of Engineers to conduct a comprehensive study focused on cumulative effects. In cooperation with the State of Montana, nongovernmental organizations, and other federal agencies, the US Army Corps of Engineers and the YRCDC have been planning and overseeing research projects to collect scientific information on environmental and socioeconomic aspects of the river. This study was designed to examine the relationships between birds and environmental factors within the riparian corridor of the Yellowstone River. Knowledge about relationships between birds and characteristics of the environment will provide a better understanding of the potential impacts of land and water management decisions that might modify the availability of particular resources within the riparian zone. Given that the same environmental factors often influence the distribution and abundance of many different types of terrestrial wildlife species, this information will also allow for a general assessment of the potential influences of management on other native riparian species.

We investigated the factors influencing community characteristics and the distribution and abundance of breeding birds along a 725 kilometer (450 mile) section of the Yellowstone River in central and eastern Montana. Birds and vegetation were surveyed within riparian habitats along braided sections of the river in order to describe patterns of bird species richness, bird occurrence, and bird abundance, and examine the factors influencing bird distribution. Our objectives were to:

1) Identify important factors influencing riparian bird communities, including characteristics of local habitat, forest cover, and land use;

2) Describe how characteristics of habitat, forest cover, and land use are distributed along the length of the river;
3) Assess the influences of habitat, forest cover, and land use on bird community characteristics and the distribution and abundance of particular species;
4) Quantify the additional effects of river location on birds, after accounting for the effects of habitat, forest cover, and land use; and
5) Examine the potential influences of Russian olive on bird species richness and abundance

STUDY AREA

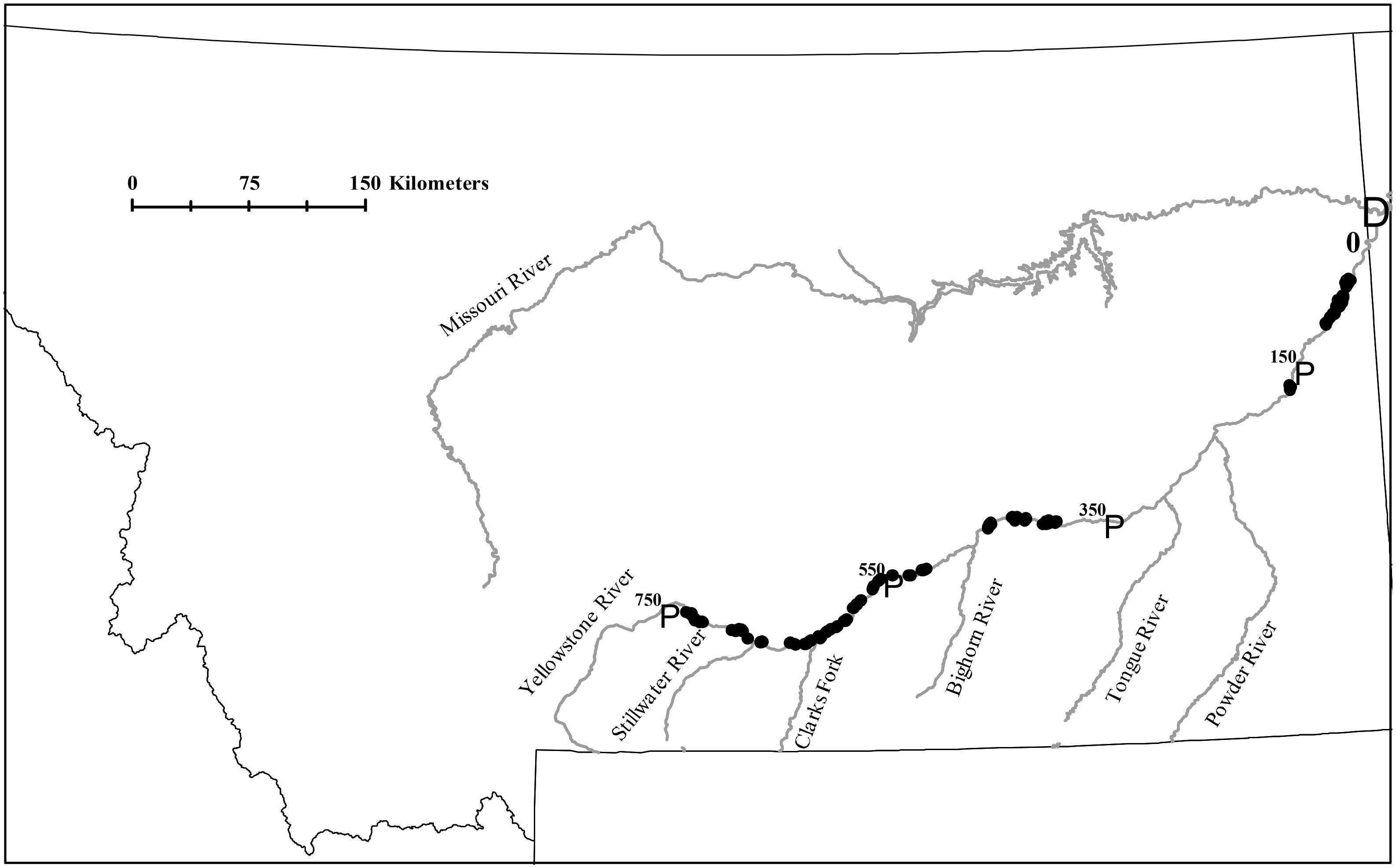
The Yellowstone River originates in the high mountains of Yellowstone National Park, flowing approximately 1125 kilometers (km; 699 miles [mi]) through the foothills of the Rocky Mountains and the Great Plains of eastern Montana to its confluence with the Missouri River in western North Dakota (Figure 1). As the river flows downstream, water volume, temperature, and turbidity increase, and the floodplain widens dramatically. Dominant land uses bordering riparian forests also change along the river, transitioning to more rural, crop-dominated landscapes in the eastern portion.

The study area (Figure 1) extends approximately 725 river km (450 river mi) from Big Timber, Montana to Sidney, Montana. (When discussing distances and locations along the river, we will refer to 'river km' or 'river mi', the distance in kilometers or miles from the mouth of the river.) Over 90% of the floodplain is privately owned, with the remaining lands owned and managed by state and federal entities (Applied Geomorphology and DTM Consulting 2004). Five major tributaries in the study area, including the Stillwater, Clarks Fork, Bighorn, Tongue, and Powder Rivers (Figure 1), contribute to changes in hydrology and sediment load along the river.

The geomorphology of the river includes reaches with multiple channels, wooded islands, and gravel bars, as well as naturally confined reaches with single, straight channels. A geomorphologic classification of the entire middle and lower river was recently completed. The study area was divided into reaches in order to identify segments of the river with similar geomorphic characteristics. Sixty-seven reaches were delineated, and were on average approximately 11 km (7 mi) in length (Applied Geomorphology and DTM Consulting 2004). Bird communities were surveyed only in reaches classified as 'multi-channel' (i.e. braided and anabranching) because the most extensive stands of riparian vegetation are located within these reaches, and because multi-channel reaches of the river are likely to be most impacted by any future river management activities. Furthermore, sampling occurred only in reaches identified as 'priority' areas (Applied Geomorphology and DTM Consulting 2004). Few multi-channel reaches existed between river kms 170 and 390 (river miles 106 and 242) due to geomorphic characteristics that confine the river to a single channel; consequently, no surveys were located in that region. For the multi-channel reaches where sampling occurred, the floodplain increased from approximately 1.75 km (1.1 mi) wide near Big Timber to four km (2.5 mi) wide near Sidney. River gradient declined from 0.2% to 0.05% slope along that same length of river (Applied Geomorphology and DTM Consulting 2004).

Riparian vegetation in multi-channel reaches consists of cottonwood forest in various stages of succession, as well as herbaceous and shrubby wetlands. For this study, we focused mostly on mature cottonwood forests (at least 50 years old) because this is the dominant habitat

Figure 1. Study area along approximately 725 kilometers of the Yellowstone River in central and eastern Montana, USA. Black dots denote locations of survey sites in riparian habitats. Vertical lines with numbers next to them show river kilometer values at those locations. The 'X' marks the mouth at river kilometer zero, where the Yellowstone flows into the Missouri River.



type within the riparian zone, and because cottonwood forests support the most diverse plant and breeding bird communities of all riparian habitats (Rumble and Gobeille 2004). Additionally, by focusing efforts in cottonwood forest, we were able to ensure that adequate samples could be attained in all types of cottonwood forest habitat.

Narrowleaf cottonwood (*Populus angustifolia*) and plains cottonwood (*P. deltoides*) dominate the overstory of riparian forests along the river. Narrowleaf cottonwood is located mostly along the upstream reaches of the river (above river km 475 [river mi 295]), while plains cottonwood is found along the entire length of the study area. Other common tree species include willow (*Salix* spp.) and green ash (*Fraxinus pennsylvanica*). Ash trees are most abundant in reaches near the mouth of the river, below river km 325 (river mi 202). Common understory shrub species include Russian olive (*Elaeagnus angustifolia*), common and western snowberry (*Symphoricarpos albus* and *S. occidentalis*), wood's rose (*Rosa woodsii*), red-osier dogwood (*Cornus stolonifera*), common chokecherry (*Prunus virginiana*), and buffaloberry (*Shepherdia canadensis*).

Main land uses within the floodplain include agriculture (crop and livestock production) and human settlement. Common crops grown within the floodplain of the Yellowstone include alfalfa, corn, sugar beets, barley, and wheat. Irrigated hayfields are also an important component of the agricultural landscape. Cattle grazing occurs seasonally within cottonwood forests and adjacent pastures, but is difficult to quantify, and is not a focus of this study. Grazing impacts to bird communities occur through the modification of habitat; therefore, any potentially confounding influences of grazing should be accounted for by considering the influence of vegetation on birds.

METHODS

Data Collection

Birds were sampled using standard fixed radius point count methods (Ralph et al. 1993). Surveys were conducted no earlier than 15 minutes after sunrise, and no later than 10 a.m. After arriving at each point count site, the observer waited for two minutes to allow the birds to acclimate to their presence. All birds seen or heard within a 60 meter radius of the point were then recorded, by species, for ten minutes. Birds that flew over, but did not stop and use the habitat, were not counted. Four researchers conducted surveys in each of 2006 and 2007. Researchers were trained in bird identification and distance estimation for two to three weeks prior to the start of official surveys. To ensure that birds outside of the 60 meter radius circle were not counted, researchers used a laser rangefinder at each site before each survey to identify the boundaries of the survey area.

A point count site was surveyed two to three times between 28 May and 9 July in both 2006 and 2007. Visits to each site were equally spaced during this time to ensure balanced coverage throughout the breeding season. To minimize bias introduced by daily patterns in bird singing behavior, each visit to a site was conducted at a different time of the morning (at least two hours earlier or later) than the previous visit. Each visit to a particular point count site was conducted by a different researcher to minimize any systematic bias resulting from differences between observers. Surveys were not conducted during bouts of heavy rain or wind. Vegetation within cottonwood forests is generally dense, so over 80% of bird observations were aural, while less than 20% were based solely on visual identification.

A random sample of survey sites was initially chosen on public and private lands using a statistical procedure called Generalized Random Tessellation Stratified Design (Stevens and Olsen 2004). Additional sites were later added (as randomly as possible) based on accessibility to private lands. Sites were located within habitat patches that were large enough to accommodate at least one point count to ensure that all bird observations at that site occurred within a single habitat type. Additionally, sites were located only within habitat patches that could be accessed by foot; consequently, islands generally were not sampled. All sites were located at least 200 meters apart. Surveys were conducted in eight counties (Carbon, Dawson, Richland, Rosebud, Stillwater, Sweet Grass, Treasure, and Yellowstone) on the lands of 60 private landowners, and thirteen parcels of public land.

Characteristics of vegetation structure and composition were measured at all point count sites. For each site, vegetation was sampled within four subplots, with the center of the subplot located 30 meters in each cardinal direction from the survey location. All trees present within an eight meter radius of the center of the subplot, and all shrub and sapling stems present within a four meter radius, were counted and recorded by species. A stem was considered a tree if the trunk was at least ten centimeters (cm) diameter at breast height (dbh). The species, abundance, and dbh class ('small' = 10-60 cm and 'large' = greater than 60 cm) were recorded for all trees. All standing dead trees (i.e. snags) that were at least one meter tall were also counted, by dbh class, within the eight meter radius subplot. A woody stem was considered a shrub or sapling if it was at least ten centimeters tall, and its dbh was less than ten centimeters. The species, abundance of stems, and height class ('small' = 10-50 cm and 'large' = greater than 50 cm tall) of all shrubs and saplings were recorded. Percent cover of the canopy that was at least five meters tall was recorded at the center of the subplot using a densiometer. A densiometer is a convex mirror that allows for the estimation of continuous (i.e. with values from 0 to 100%) canopy cover. Data collected at the four subplots of a particular point count site were then averaged to get one value for each variable for each site.

Predictor Variables

The vegetation data collected at each point count site were subjected to cluster analysis in order to identify sites with similar vegetation characteristics that represented distinct habitat types (Kent and Coker 1992). Twenty-six variables representing compositional and structural characteristics of the vegetation were used for analysis (Table 1). Data were partitioned into clusters in two steps. First, all point count sites were subject to analysis, and three habitat types were identified: cottonwood forest, shrubland, and grassland. Cottonwood forest sites were then subject to analysis a second time to identify distinct types of cottonwood habitat; five unique habitat types were identified. Ecological attributes of each habitat type were evaluated based on relevant characteristics of the overstory and understory vegetation. To describe differences between habitat types, mean values and 95% confidence intervals (CIs) of important vegetation variables were compared. The 95% confidence intervals represent the range of values where we are 95% confident that the true mean resides.

Percent forest cover surrounding each point count site was quantified through aerial photo interpretation. Digital color infrared aerial photos of the riparian zone, taken in August 2001, were used to quantify the amount of forest cover within a 200-m radius of each point count location. Using ArcGIS software (ESRI 2006), a gridded circle was overlaid on each site, and the percentage of squares that intersected woody canopy cover was recorded. Percent forest cover at sites ranged from 3% to 93% (Table 2).

Aerial photos were also used to derive two variables that represented dominant land uses within the floodplain. First, the locations of all human settlements within the sampled reaches of the river were digitized. A settlement may be either a house or an outbuilding (as it is difficult to discriminate between these types of structures in an aerial photo), and had to have a driveway leading to it to be included in the dataset. The distance from each point count site to the nearest three settlements was then averaged to get a mean distance to settlement for each site. Second, the distance to the nearest irrigated crop field was measured for each site. Only irrigated crop fields were included because it was impossible to discriminate between dryland crops and rangeland on aerial photos. Both of these variables were log-transformed to reduce the effect of outliers in the data. Values of log distance to settlement ranged from 4.49 to 7.90, while values of log distance to crop ranged from 4.08 to 8.57 (Table 2).

River kilometer was used to quantify the location of a site along the length of the river. River kilometers are measured along an approximation of the centerline of the main channel, with km 0 located at the mouth of the river and increasing in the upstream direction (Applied Geomorphology and DTM Consulting 2004). River location of sites ranged from km 63 to km 727 (mi 39 to 452; Table 2).

Data Analysis

Distributions of Predictor Variables. To assess the distributions of habitat type, forest cover, and land use variables along the river, the association of each variable with river location was quantified. For the categorical habitat variable, mean river kilometer and a 95% CI were calculated for each habitat type. If habitats are differentially distributed across reaches of the river rather than evenly distributed along its length, mean river kilometer should differ between habitat types. For the three continuous variables, linear regression was used to quantify the influence of river kilometer on each variable; both linear and quadratic relationships were examined, and the relationship with the highest adjusted r^2 value (a measure of the amount of variation explained by the variables in the model) is reported.

Bird Species Richness. The average number of bird species observed across all visits was calculated for each survey site. Multiple measures of bird richness were quantified: total richness; richness of Neotropical migrant (NTM) species; and richness of species in different foraging and nesting guilds. Total richness was quantified using all 64 species. NTM richness was quantified using the 34 species that winter south of the US in Central and South America (Appendix 1). NTM species were included in analysis because they are of specific conservation and management concern due to estimated population declines for many of the species. Means and 95% CIs were calculated for total and NTM richness to identify differences between habitat types. To examine variation in richness along the length of the river, linear regression was used to quantify the relationship between mean richness and river location for sites within each habitat type. Adjusted r^2 values and p-values for parameter estimates were reported.

Guild richness was calculated using 48 species that were observed at more than one cottonwood forest site over the two years. A ‘guild’ is an association of species that use resources in a similar way. Analysis of guild richness may provide additional information about the types of species that are using different habitat types. Each species was assigned to a nesting and foraging guild according to published life history accounts (Appendix 1). Four foraging guilds were identified based on where foraging occurs: FGND included species that forage primarily on the ground (15 species), FLOW included species that forage either on the ground or

Table 1. Structural and compositional vegetation variables included in cluster analysis for identifying distinct habitat types. The abundance of each taxonomic variable was included after being grouped into structural class types, with an 'X' indicating the class types included in analysis for each variable. Canopy cover was included as a percentage value.

Variable	Scientific Name/ Description	Variable Class Type			
		Small shrub	Large shrub	Small dbh tree	Large dbh tree
Russian Olive	*Elaeagnus angustifolia*	X	X	X	
Green Ash	*Fraxinus pennsylvanica*	X	X	X	
Rocky Mountain Juniper	*Juniperus scopulorum*	X	X	X	
Saltcedar	*Tamarix chinensis*	X	X		
Snowberry species	*Symphoricarpos albus + S. occidentalis*	X	X		
Big Sagebrush	*Artemisia tridentata*	X	X		
Other Native Shrubs	*Rosa woodsii + Cornus stolonifera + Prunus virginiana + Rhus trilobata + Ribes viscosissimum + Ribes aureum + Shepherdia canadensis + Populus angustifolia + P. deltoides*	X	X		
Narrowleaf Cottonwood	*P. angustifolia*			X	X
Plains Cottonwood	*P. deltoides*			X	X
Other Native Trees	*Salix spp. + Acer negundo+ Ulmus americana*			X	X
Snags	All standing dead trees ≥ 1 m tall			X	X
Canopy Cover	Percent cover ≥ 5 m tall, as recorded with densiometer				

Table 2. Summary statistics for continuous predictor variables.

Predictor Variable	Summary Statistic				
	Min	1st Quartile	Mean	3rd Quartile	Max
Percent forest cover	2.67	30.53	47.43	63.74	92.75
Log distance to crop	4.08	5.18	5.90	6.51	8.57
Log distance to settlement	4.49	6.40	6.74	7.17	7.90
River kilometer	62.76	98.17	414.70	618.80	727.40

in shrubs (11 species), FCAN included species that forage either in shrubs or higher canopy layers (10 species), and FAIR included species that forage by catching insects on the wing (7 species). A fifth foraging guild was identified that included species that forage by probing for insects on the trunk or branches of trees (FTRE). However, sample sizes were very small, with only five species included in this guild; consequently, this guild was not used in analysis. Four nesting guilds were identified based on where nesting occurs: NGND included species that place their nests on (or very close to) the ground (10 species), NLOW included species that nest primarily in shrubs or low canopy (< 5 meters above ground; 17 species), NMSC included species that nest in the mid-story and high canopy (> 5 meters above ground; 9 species), and NCAV included species that nest in cavities of live or dead trees (11 species). Means and 95% CIs were calculated for total and NTM richness to identify differences between cottonwood habitat types. Guild richness within grassland and shrub habitats, and variation in guild richness along the length of the river were not examined because sample sizes within guilds were too small for meaningful analyses.

Bird Occupancy. The influences of habitat, forest cover, and land use variables on the distribution of birds were quantified by estimating the proportion of sites occupied by each species. While the presence of a particular species is evidence that a site is occupied by that species, its 'absence' could mean that it is either 1) not present at the site, or 2) present, but was not detected by the researcher. Differences in singing rates and other behaviors may result in detection rates that vary across species, while differences in environmental conditions across sites and over time may result in variable detection rates for a particular species. Given that the imperfect detection of a species may result in spurious conclusions about occupancy (e.g. a species that does not sing often is reported to have low occupancy, when actual occupancy is much higher), we used an approach that uses logistic regression to simultaneously model occupancy and detection rates to provide corrected estimates of species occupancy that account for imperfect detectability (MacKenzie et al., 2002, 2006).

Detection rates were modeled as either a function of time of season and/or habitat, or as constant across all visits and sites. Time of season may be an important determinant of detection probability because singing behavior often fluctuates as a function of the stage of the breeding cycle. Habitat characteristics, particularly vegetation density and structural diversity, may influence detection probability through the modification of bird behavior in particular habitats, or by altering a researchers ability to detect birds (Ganzalo-Turpin et al. 2008). Detection rates are used to adjust occupancy rates to account for imperfect detectability.

Adjusted occupancy rates were estimated only for species that were observed at ≥ 20% of sites in both 2006 and 2007. Additionally, only NTM species, sparrows, and non-native species were included in analysis in order to focus on species of general conservation or management concern. Consequently, eleven species were used for occupancy analysis (Table 3). American redstart (*Setophaga ruticilla*), lazuli bunting (*Passerina amoena*), and black-headed grosbeak (*Pheucticus melanocephalus*) were excluded due to inconsistencies in identification that were exhibited by researchers in the field. Due to limited sample sizes of shrubland and grassland habitats, only cottonwood forest sites were used for occupancy analysis.

Program MARK (White and Burnham 1999) was used to model occupancy rates (ψ). Occupancy rates range from zero to one, and represent the probability that a site will be occupied by a species, after accounting for the detection probability of the species. To quantify the effects of predictor variables on ψ, model selection methods were first used to identify which variables were most influential on ψ for each species. A list of candidate models was developed, with each model including a different combination of predictor variables. The set of candidate models included five variables: habitat type (HAB), forest cover (FCOV), log mean distance to human settlement (LNSETT), log distance to crop (LNCROP), and river kilometer (RKM). Candidate models were developed based on questions about the individual and combined influences of local habitat, forest cover, and land use. The additional influence of river kilometer was also considered. The same candidate model set was used for all species (Table 4).

Table 3. Fourteen species included in occupancy and abundance analysis. General habitat associations and brown-headed cowbird host status were summarized from published life history accounts for each species, and expected relationships with predictor variables were derived from these accounts. A '+' denotes an expected positive relationship between occupancy or abundance and the predictor variable, while a '--' denotes an expected negative relationship. See Appendix 1 for scientific names.

Species	Foraging Guild[1]	Nesting Guild[2]	General Habitat Association	Cowbird Host Status	Expected Relationship with Predictor Variables: Forest Cover	Distance to Settlement	Distance to crop	Citation
Occupancy								
Common Yellowthroat	FLOW	NGND	Early successional dense shrub	Frequent	--	+	--	Guzy and Ritchison, 1999
European Starling	FGND	NCAV	Avoids large expanses of forest	Rare	--	+	--	Cabe, 1993
Gray Catbird	FLOW	NLOW	Edge habitat with dense understory	Rare	--		--	Cimprich and Moore, 1995
Least Flycatcher	FAIR	NLOW	Semi-open large, contiguous forest	Infrequent	+			Briskie, 1994
Ovenbird	FGND	NGND	Large tracts of contiguous forest	Frequent	+	+		Van Horn and Donovan, 1994
Red-eyed Vireo	FCAN	NLOW	Forest interior, but uses fragments	Frequent	+	+		Cimprich et al., 2000
Song Sparrow	FLOW	NGND	Early successional shrub	Frequent	--	+	--	Arcese et al., 2002
Spotted Towhee	FLOW	NGND	Early successional shrub and scrub	Frequent	--	+	--	Greenlaw, 1996
Warbling Vireo	FCAN	NMSC	Mature semi-open woodlands	Frequent	+	+		Gardali and Ballard, 2000
Western Wood-pewee	FAIR	NMSC	Open forest with large trees and edge	Infrequent	--		--	Bemis and Rising, 1999
Yellow-breasted Chat	FLOW	NLOW	Open forest with dense shrub	Frequent	--	+	--	Eckerle and Thompson, 2001
Abundance								
Brown-headed Cowbird	FGND	--	Grassland-woodland edges	NA	--	--	--	Lowther, 1993
House Wren	FLOW	NCAV	Open, shrubby woodlands	No	--		--	Johnson, 1998
Yellow Warbler	FCAN	NLOW	Early successional shrub	Frequent	--	+	--	Lowther et al., 1999

[1] Foraging guilds, by location of foraging activity: FGND = ground, FLOW = ground or shrubs, FCAN = shrubs or canopy, FAIR = on the wing
[2] Nesting guilds, by location of nest: NGND = on/close to ground, NCAV = in cavities, NLOW = shrubs or low canopy, NMSC = midstory or high canopy

Table 4. Candidate set of models for examining the factors affecting occupancy rate (ψ) or abundance for fourteen riparian bird species.

Modeling	Description	Model Structure
Step 1: Determine best forms of univariate relationships	Percent forest cover (FCOV)	$\beta_0+\beta_1$*FCOV $\beta_0+\beta_1$*FCOV+ β_2*FCOV^2
	Average distance to nearest house (LNSETT)	$\beta_0+\beta_1$*LNSETT $\beta_0+\beta_1$*LNSETT+ β_2*LNSETT^2
	Log distance to nearest crop (LNCROP)	$\beta_0+\beta_1$*LNCROP $\beta_0+\beta_1$*LNCROP+ β_2*LNCROP^2
	River location (RKM)	$\beta_0+\beta_1$*RKM $\beta_0+\beta_1$*RKM+ β_2*RKM^2
Step 2: Determine important factors influencing ψ or abundance	Best models from univariate modeling in Step 1 plus model including habitat type (HAB)	β_0+HAB β_0+FCOV$_{best}$ β_0+LNSETT$_{best}$ β_0+LNCROP$_{best}$ β_0+RKM$_{best}$
	Habitat and forest cover	β_0+HAB+FCOV$_{best}$
	Land use	β_0+LNSETT$_{best}$+LNCROP$_{best}$
	Forest cover and land use	β_0+FCOV$_{best}$+LNSETT$_{best}$ β_0+FCOV$_{best}$+LNCROP$_{best}$ β_0+FCOV$_{best}$+LNSETT$_{best}$+LNCROP$_{best}$
	Habitat and land use	β_0+HAB+LNSETT$_{best}$ β_0+HAB+LNCROP$_{best}$ β_0+HAB+LNSETT$_{best}$+LNCROP$_{best}$
	Habitat, forest cover, and land use	β_0+HAB+FCOV$_{best}$+LNSETT$_{best}$ β_0+HAB+FCOV$_{best}$+LNCROP$_{best}$ β_0+HAB+FCOV$_{best}$+LNSETT$_{best}$+LNCROP$_{best}$
	Additional influence of river location	All previous models in Step 2 +RKM$_{best}$

Information theoretic approaches were used to identify the most parsimonious models (i.e. models with as few parameters as necessary; Burnham and Anderson 2002). All candidate models were compared using Akaike Information Criteria corrected for small sample sizes (AICc; Burnham and Anderson 2002). Model selection occurred in two steps. First, for each continuous variable, a model with only a linear term was compared to a model that included a quadratic term (Table 4), and the best form of the univariate relationship was identified as the model with the lowest AICc score. These 'best' models for each continuous variable were then included in the next step of model selection. In step two, candidate models including various combinations of all predictor variables were compared. Models within 2 AICc units of the model with lowest AICc score (i.e. ΔAICc score ≤ 2) were considered 'top-ranking'. All predictor variables included in top-ranking models were considered to be influential on ψ.

Tests were conducted to assess the fit of the most-parameratized models for each species. A goodness-of-fit method designed for occupancy analysis, described by MacKenzie and Bailey (2004), was available in the software program PRESENCE (Hines 2006). Quasi-AICc (QAICc) scores were used to compare candidate models when overdispersion was estimated to be greater than one (MacKenzie et al. 2006).

Once the influential variables were identified through model selection, the effects of those variables on ψ were examined for each species. Parameter estimates and 95% CIs were examined for each continuous variable to assess the nature and strength of its effect on ψ. For the categorical habitat variable, estimates of ψ and 95% CIs were compared across habitat types. Additionally, cumulative model weight (($\sum w_i$), was calculated for each predictor variable. Cumulative model weight is the sum of the AICc or QAICc weights of all models in the candidate model set that include a particular variable. (Q)AICc weights represent the weight of the evidence that a particular model is actually the model that best fits the data (Burnham and Anderson 2002). Therefore, cumulative model weight may be interpreted as a measure of the strength of the evidence that a particular variable is relatively influential on ψ for a given species.

Occupancy rates were estimated separately in each year for each species, and results are reported for each year. This was done because occupancy models that incorporate multiple years of data in a single analysis were not appropriate for our data (MacKenzie et al. 2006). Therefore, years were analyzed separately to avoid problems in the estimation of the variance of ψ that may arise due to pseudoreplication, because most of the same sites were visited over the two years. For model selection, models for ψ were constrained to have the same structure for both 2006 and 2007, so that the variables identified in top-ranking models were the same in both years. This was done because we expected the influences of covariates for ψ to largely reflect life-history traits of a particular species, which should not change over a two-year time period.

Bird Abundance. Yellow warblers (*Dendroica petechia*) and house wrens (*Troglodytes aedon*) were observed at 99% and 97% of sites respectively, so were excluded from occupancy analysis. Brown-headed cowbirds (*Molothrus ater*) were also excluded because this species is an exclusive nest parasite and does not hold a breeding territory, which may lead to violations of the assumptions of occupancy modeling (MacKenzie et al. 2006). These three species were instead modeled using linear regression, with mean abundance as the response variable. Abundance was averaged across visits at a site for each year.

The framework for abundance modeling was very similar to occupancy modeling. Model selection was used to examine the influences of HAB, FCOV, LNSETT, LNCROP, and RKM on the mean abundance of each species. Selection occurred in two steps, with the form of univariate relationships for each variable first determined, followed by a comparison of the AICc scores of candidate models to assess the individual and combined influences of habitat, forest cover, land use, and river location on abundance. The same candidate model list that was used for occupancy (Table 4) was used for yellow warblers and house wrens, with one exception. Models were not run separately for each year; instead, year was included as an additive effect in all candidate models. This was done because estimates of abundance were expected to vary across years due to natural fluctuations in population numbers, but the relative influence of each variable on abundance was not expected to change across years.

The candidate model list used for brown-headed cowbirds in Step 2 of model selection was different than the list used for the other species (Table 5). Models included the variables FCOV, LNSETT, and RKM, because these are the factors that were expected to be important for cowbirds based on their life history traits. Models differed in two ways from the candidate model set used for the other species. First, cowbirds do not forage in cottonwood forest, but instead travel far distances to feed in farmsteads and human settlements (Tewksbury et al. 1998). There is evidence that the relationship between cowbirds and human settlement is stronger in areas of low density of settlement, where these high-quality feeding opportunities are a limited resource (Tewksbury et al. 2006). Mean distance to settlement decreases steadily in the upstream direction from the mouth of the river, so that different sections of the river experience different degrees of human settlement (see Results). Consequently, we would expect that

Table 5. Additional candidate set of models for examining the factors affecting abundance of brown-headed cowbirds. Step 1 is the same as described in Table 4. Step 2 of modeling for cowbirds was developed to examine the influences of forest cover (FCOV), log distance to human settlement (LNSETT), log distance to crop (LNCROP), and host abundance (HOST) on cowbird abundance. Region (REG) was included to examine interactions between region of the study area and HOST or LNSETT.

Modeling	Description	Model Structure
Step 2: Determine important factors influencing abundance of Brown-headed cowbirds	Models from univariate modeling in Step 1	β_0+FCOV_{best}
		$\beta_0+LNSETT_{best}$
		$\beta_0+LNCROP_{best}$
		β_0+RKM_{best}
	Land use	$\beta_0+LNSETT_{best}+REG+LNSETT_{best}*REG$
		$\beta_0+LNSETT_{best}+LNCROP_{best}$
		$\beta_0+LNSETT_{best}+LNCROP_{best}+REG+LNSETT_{best}*REG$
	Forest cover and land use	$\beta_0+FCOV_{best}+LNSETT_{best}+LNCROP_{best}$
		$\beta_0+FCOV_{best}+LNSETT_{best}+LNCROP_{best}+ REG+LNSETT_{best}*REG$
		$\beta_0+FCOV_{best}+LNSETT_{best}$
		$\beta_0+FCOV_{best}+LNSETT_{best}+REG+LNSETT_{best}*REG$
		$\beta_0+FCOV_{best}+LNCROP_{best}$
	Influence of host abundance	$\beta_0+HOST+REG+HOST*REG$
		$\beta_0+FCOV_{best}+HOST+REG+HOST*REG$
		$\beta_0+LNSETT_{best}+HOST+REG+HOST*REG$
		$\beta_0+LNSETT_{best}+HOST+REG+HOST*REG+ LNSETT_{best}*REG$
		$\beta_0+LNCROP_{best}+HOST+REG+HOST*REG$
		$\beta_0+LNSETT_{best}+LNCROP_{best}+HOST+REG+HOST*REG$
		$\beta_0+LNSETT_{best}+LNCROP_{best}+HOST+REG+HOST*REG+ LNSETT_{best}*REG$
		$\beta_0+LNSETT_{best}+LNCROP_{best}+HOST+REG+HOST*REG$
		$\beta_0+FCOV_{best}+LNSETT_{best}+LNCROP_{best}+HOST+REG+HOST*REG$
		$\beta_0+FCOV_{best}+LNSETT_{best}+LNCROP_{best}+HOST+REG+HOST*REG+ LNSETT_{best}*REG$
		$\beta_0+FCOV_{best}+LNSETT_{best}+HOST+REG+HOST*REG$
		$\beta_0+FCOV_{best}+LNSETT_{best}+HOST+REG+HOST*REG+ LNSETT_{best}*REG$
		$\beta_0+FCOV_{best}+LNCROP_{best}+HOST+REG+HOST*REG$
	Additional influence of river location	$\beta_0+FCOV_{best}+RKM_{best}$
		$\beta_0+LNSETT_{best}+RKM_{best}$
		$\beta_0+LNCROP_{best}+RKM_{best}$
		$\beta_0+LNSETT_{best}+LNCROP_{best}+RKM_{best}$
		$\beta_0+FCOV_{best}+LNSETT_{best}+LNCROP_{best}+RKM_{best}$
		$\beta_0+FCOV_{best}+LNCROP_{best}+RKM_{best}$
		$\beta_0+FCOV_{best}+LNSETT_{best}+RKM_{best}$

cowbirds may respond to human settlement differently in different sections of the river. This potential response was included in candidate models by adding a categorical variable (REG) that divides the river into four sections (river kms 63 – 170 [mi 39 – 106]; 388 – 455 [mi 241 – 283]; 513 – 606 [mi 319 – 377]; and 611 – 727 [mi 380 – 452]), and an interaction term between LNSETT and REG (Table 5). REG and RKM both represent river location and are highly correlated, and were therefore never entered into the same model (Table 4). Second, the abundance of host species at a site has been demonstrated as an important influence on cowbird abundance, so a variable that represents host abundance (HOST) was included in candidate models. There is evidence that the relationship between cowbird parasitism rates and the abundance of host species is strongest in areas where human density is highest and the abundance of feeding opportunities is not a limiting factor (Tewksbury et al. 2006). Therefore, an interaction between HOST and REG was included in models (Table 5).

R software (R Development Core Team 2008) was used for all abundance analyses. Model selection was performed on fixed-effects linear models. After top-ranking models were identified, autocorrelation within the data was accounted for using mixed fixed- and random-effects models (Pinheiro and Bates 2000). Random effects were added to each top-ranking model to account for spatial autocorrelation between points that are close together, and temporal autocorrelation for observations between years at a point.

Expected Influences of Predictor Variables. Although modeling was exploratory in nature, the influence of each variable on ψ or abundance will likely reflect life history traits of a species. We therefore discuss the results for each species in the context of guild membership in order to provide insight about potential reasons for observed patterns in habitat use. The same guild designations were used for species as were used for quantifying guild richness (Table 3). Given that local habitat has been identified as one of the most important variables influencing the distribution and abundance of riparian birds (Stauffer and Best 1980, Strong and Bock 1990, Farley et al. 1994, Miller et al. 2004), HAB was expected to be an important influence on ψ and abundance for all species, with two exceptions. Ovenbirds are an interior forest species, found largely in areas of dense forest cover (Table 3). Given that riparian forests are very patchy in nature and dense forest may be a limited resource, local habitat may be less important to this species. Local habitat may also be less important to European starlings because they forage in bordering open areas and fields, not in forest habitats. Additionally, starlings nest in tree cavities (Table 3), which are likely not a limited resource in any of the mature cottonwood forest habitat types.

The amount of forest cover in the surrounding riparian zone may be important to a species based on whether it prefers forest interior or edge habitats (Trczcinski et al. 1999). We expected that those species with an affinity for forest edges (based on published life history accounts) would have a negative relationship with FCOV, while forest interior species would have a positive relationship with FCOV (Table 3).

There is evidence that Brown-headed cowbirds, which parasitize the nests of many riparian species, are positively associated with areas of human settlement (Tewksbury et al. 1998, Tewksbury et al.2006). We therefore expected that LNSETT would have a positive effect on species that are frequent cowbird hosts (because increasing values of LNSETT indicate that human settlement is farther from the riparian zone). We also expected that European starlings would have a positive relationship with LNSETT because increased densities of human settlement may cause a decline in the area of open pasture and rangeland that starlings use for foraging (Table 3).

Agricultural fields adjacent to the riparian zone provide open areas for foraging and an abrupt and continuous forest edge in an otherwise patchy landscape. Therefore, we expected that species that prefer to forage in open fields and species that have a strong association with forest edges would have a negative relationship with LNCROP, because decreasing values of LNCROP indicate that crop fields are closer to riparian forest habitats (Table 3). There is also evidence that human settlement and agriculture influence predator communities in adjacent riparian zones. However, relationships between nest predation and land use are often complex, and are manifest through measures of productivity (Tewksbury et al. 1998, 2006). Therefore, it would be difficult to predict the influence of land use in the context of productivity based only on occupancy or abundance data.

The candidate model set for Brown-headed cowbirds was developed to examine the influences of forest cover, land use, and host abundance on cowbird abundance (Table 5). I expected that cowbird abundance would be negatively related to LNSETT (i.e. higher abundance where LNSETT is low and human settlement is closer to the riparian zone; Table 3), and that this relationship would be stronger near the mouth of the river where human settlement is least dense and feeding opportunities are a limited resource (Tewksbury et al. 2006). Furthermore, I expected cowbird abundance to be positively related to host abundance, as cowbirds would be more likely to occupy areas with more opportunities for parasitism.

Russian Olive and Bird Abundance or Richness. The influence of Russian olive and other habitat characteristics was investigated for total species richness, richness of NTM species, and mean abundance of five common NTM species, including yellow warbler, house wren, least flycatcher (*Empidonax minimus*), yellow-breasted chat (*Icteria virens*), and western wood-pewee (*Contopus sordidulous*). Linear regression was used to quantify relationships between richness or mean bird abundance and the abundance of five vegetation variables: small native shrub, large native shrub, small native tree, large native tree, and Russian olive. Percent canopy cover and river kilometer were also included in models. All variables were included in a single model with total richness as the response, a single model with NTM richness as the response, and a single model with mean abundance as the response for each species. Parameter estimates and p-values for those estimates were examined to identify the strength and nature of the influence of each variable on mean abundance. River location and vegetation variables besides Russian olive were included in models to allow for the assessment of the influence of Russian olive while simultaneously accounting for the influence of other variables. This reduces the incidence of spurious results due to correlations between Russian olive and other environmental variables.

RESULTS

Classification of Habitat Types

Vegetation data were collected at 304 survey sites in 21 reaches along the river. The number of sites sampled in a reach ranged from two to greater than 40 (Figure 2a, Appendix 2). In the initial cluster analysis, 234 sites were identified as cottonwood forest (CWFOREST), 40 sites as shrubland (SHRUB), and 30 sites as grassland (GRASS). The grassland sites had no woody stems or canopy cover (Figure 3, Table 6). The shrubland sites had few trees (Figures 3a, 3b), but a large amount of variation in the abundance of native shrubs (Figures 3c, 3d) and Russian olive (Figure 3e). Due to the larger sample size, cottonwood sites were well-distributed along the river. Most reaches sampled had at least five cottonwood sites, and many had more than ten. However, the number of sites was lower in the middle reaches of the river (Figure 2a). Sample sizes for grassland and shrubland sites were low in each reach. All but one reach had fewer than five grassland sites, and many had zero or one; this was especially true for reaches near the mouth of the river (Figure 2a). Most of the shrubland sites were located in the eastern region of the study area; reaches in the west generally had zero or one site (Figure 2a).

When the cottonwood sites were subjected to a second cluster analysis, five habitat types were identified (DC.OPENRO, MC.OPENSH, MC.DENSH, MC.LOWSH, and OC.GRASS).

These habitat types encompassed a gradient of changing canopy and understory conditions, ranging from cottonwood forest with an open canopy and few trees and shrubs, to forest with higher canopy cover and a dense understory of native shrubs. Table 6 provides a complete description of each habitat type. Structural differences in vegetation characteristics were evident between habitat types. The abundance of small and large dbh trees (Figures 3a, 3b), small and large native shrubs (Figures 3c, 3d), and Russian olive stems (Figure 3e), all differed to some degree between habitat classes. Percent canopy cover also differed across habitat types (Figure 3f). Cottonwood habitat types were generally evenly distributed along the river, but the number of sites within each reach for each habitat type was often very low (Figure 2b). This was especially true for the habitats with smaller sample sizes (Table 6).

Distribution of Predictor Variables

Distribution along the river was examined for habitat, forest cover, and land use variables. The distribution of habitat types was assessed only for cottonwood forest sites. If habitat types were distributed randomly across sites along the length of the river, the mean river kilometer for each type should be similar to the mean of all sites. Mean river kilometer of all sites was 411 km (255 mi) upstream from the mouth. Habitat types were generally evenly distributed along the river and had similar mean river kilometer values, with the exception of MC.LOWSH (Figure 4). Sites within the MC.LOWSH habitat had on average a lower river kilometer value (mean RKM = 224.60, CI: 155.00, 294.21) than the other four habitat types (mean RKMs: DC.OPENRO = 426.06, CI: 361.39,490.74; MC.OPENSH = 483.92, CI: 405.12,562.72; MC.DENSH = 416.32, CI: 364.51,468.12; OC.GRASS = 480.64, CI: 409.89,551.40), and mean river kilometer for MC.LOWSH was much lower than the mean value of all sites (Figure 4). This suggests that MC.LOWSH sites were generally distributed closer to the mouth of the river, while the other four habitat types were distributed relatively evenly along the length of the river.

There was little evidence that FCOV varied along the river (Figure 5a); the relationship between FCOV and RKM was linear and flat ($p = 0.69$). A quadratic relationship existed between LNCROP and RKM (p of quadratic term = 0.01), with distance to the nearest irrigated crop field increasing above river kilometer 500 (Figure 5b). However, the variation in LNCROP that was explained by river location was minimal ($r^2_{adj} = 0.07$).

The log mean distance to human settlement was the only predictor variable that was strongly correlated with river location ($r^2_{adj} = 0.40$, $p << 0.001$). LNSETT decreased linearly in the upstream direction from the mouth of the river (Figure 5c), suggesting that settlement was located closer to the riparian zone in the western part of the study area. This was likely due to the smaller area of the floodplain in the upstream portion of the river, and the higher density of houses found within the floodplain there.

Figure 2. Number of study sites within a) three main habitat types (CWFOREST, SHRUB, and GRASS), and b) five cottonwood habitat types (DC.OPENRO, MC.OPENSH, MC.DENSH, MC.LOWSH, and OC.GRASS) within reaches along the river. Reaches are ordered by their spatial location; reach d12 is closest to the mouth of the river (i.e. river kilometer 0) at the eastern end of the study area, while reach a07 is at the western end of the study area. Reaches vary in length, but are on average 11 kilometers long.

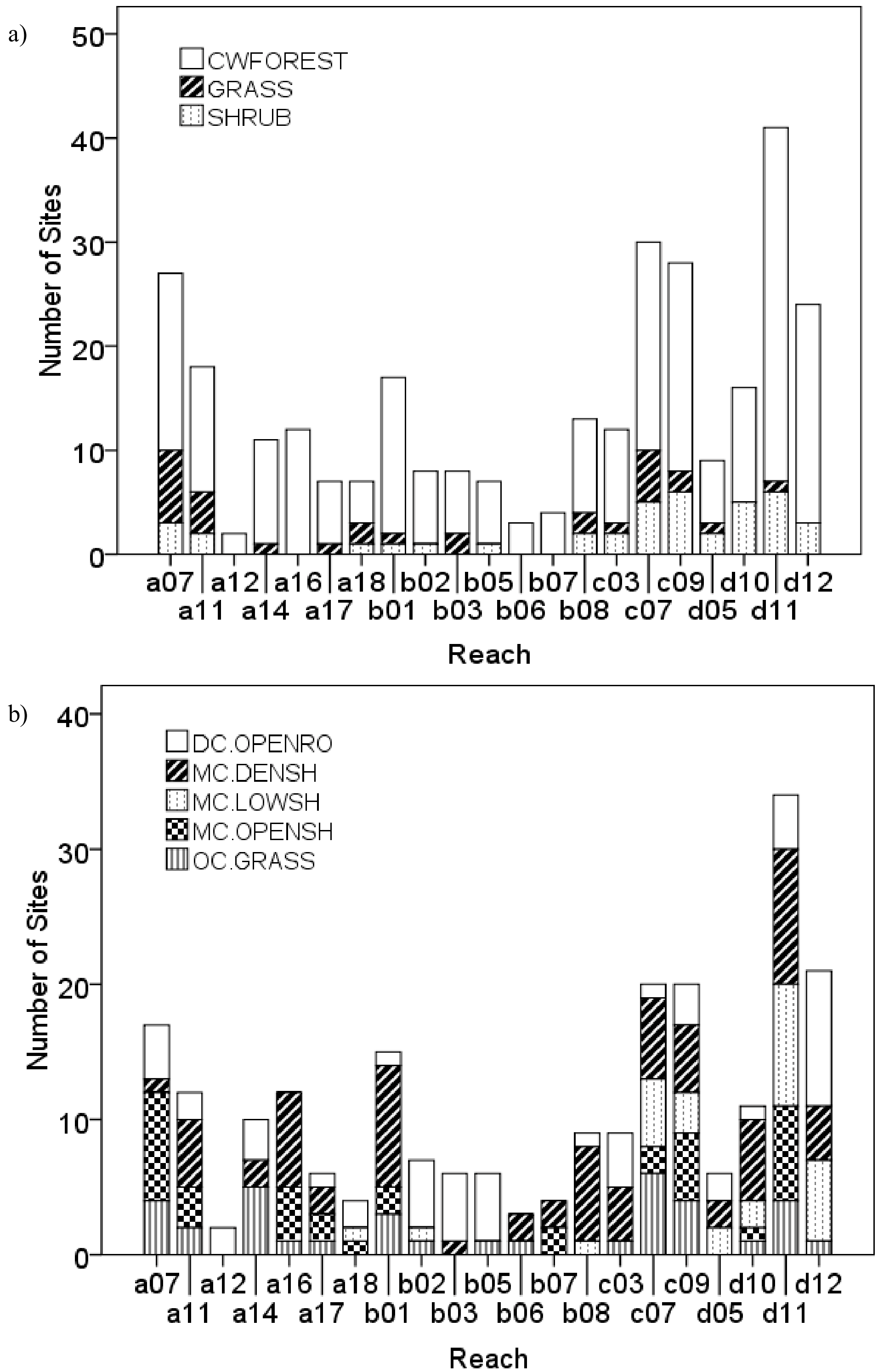
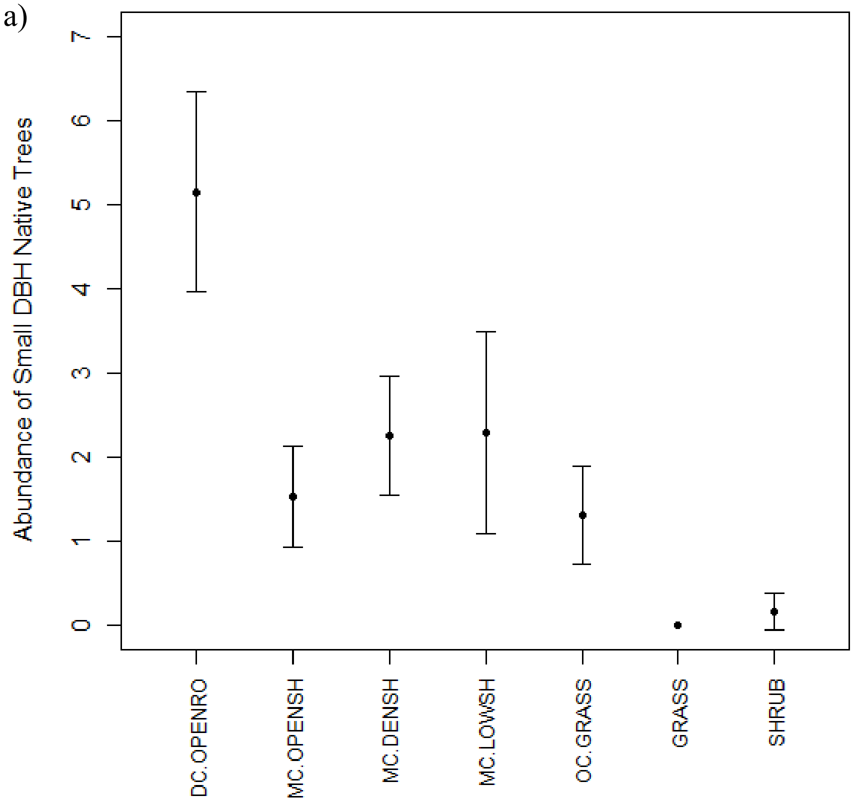


Figure 3. Vegetation characteristics of the sites within cottonwood forest (DC.OPENRO, MC.OPENSH, MC.DENSH, MC.LOWSH, and OC.GRASS), shrubland (SHRUB), and grassland (GRASS) habitat types. Points represent means and error bars represent 95% confidence intervals for a) native trees with small diameter at breast height (dbh), b) native trees with large dbh, c) native shrubs < 50 cm tall, d) native shrubs > 50 cm tall, e) Russian olive shrubs and trees, and f) percent canopy cover.

a)



b)

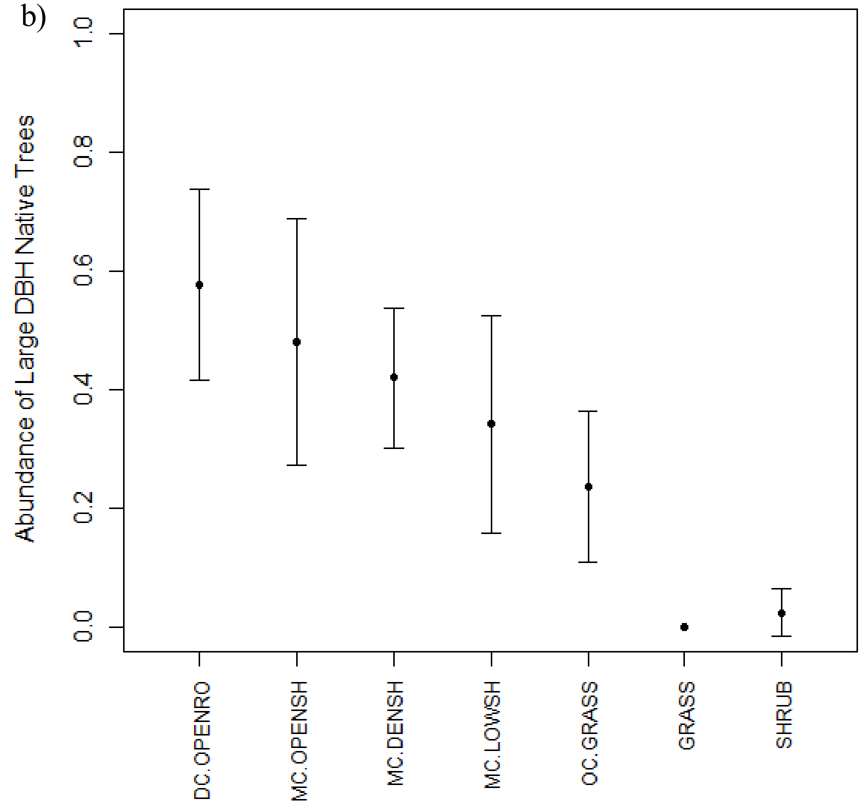
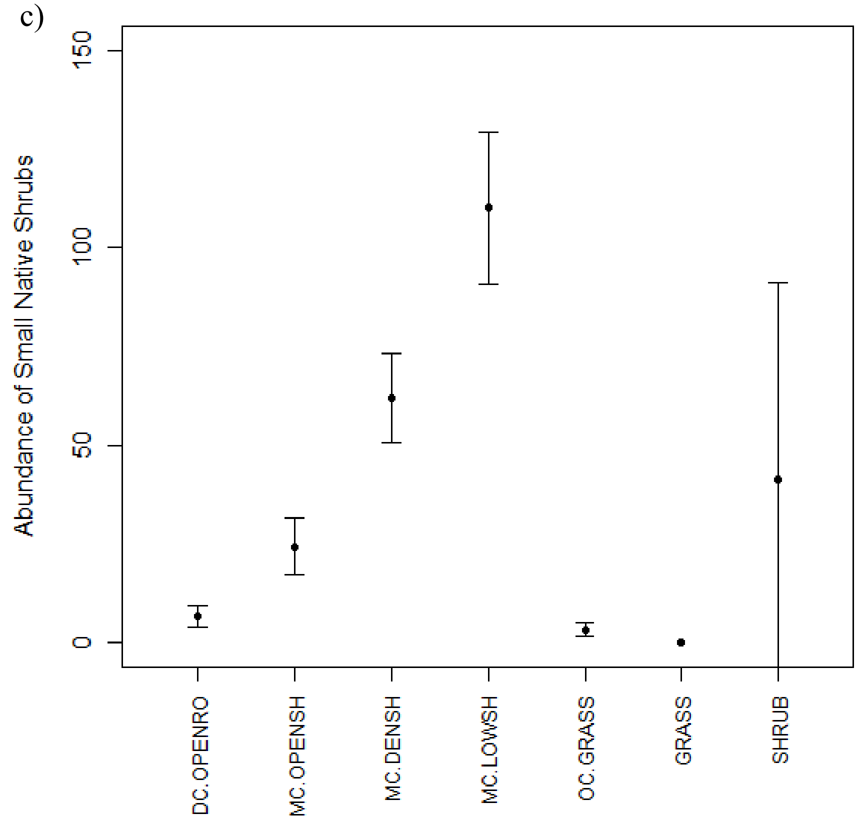


Figure 3 continued.

c)



d)

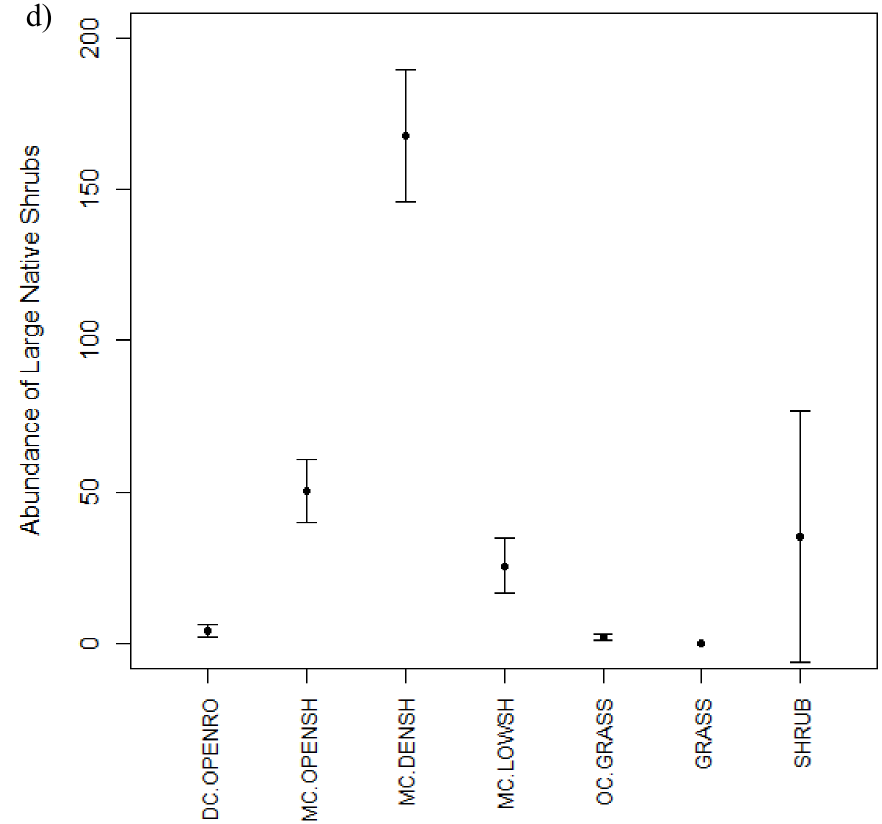
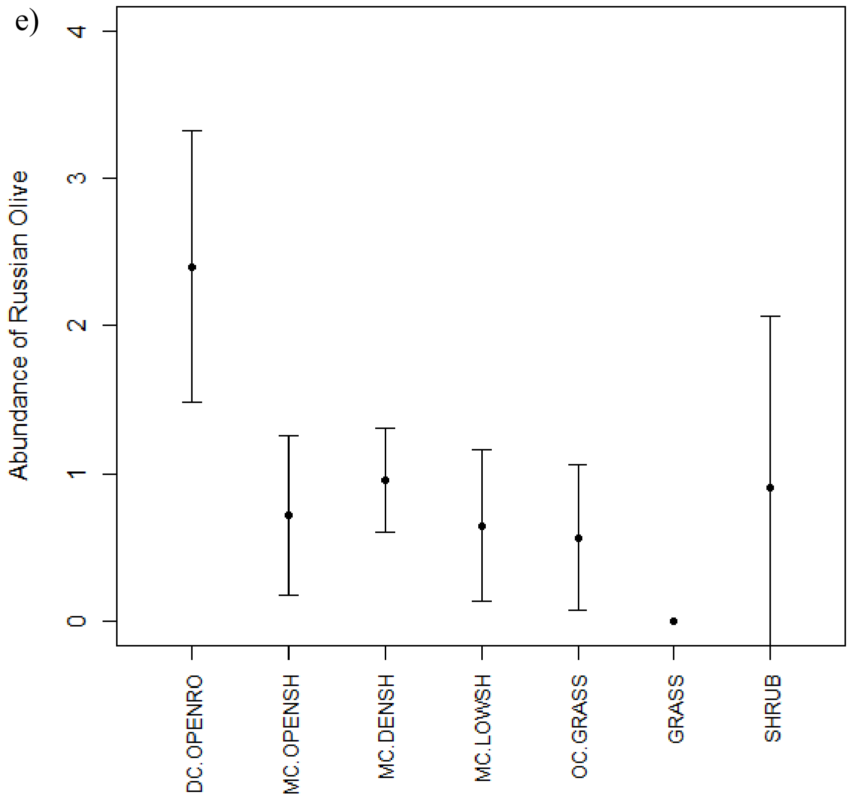


Figure 3 continued.

e)



f)

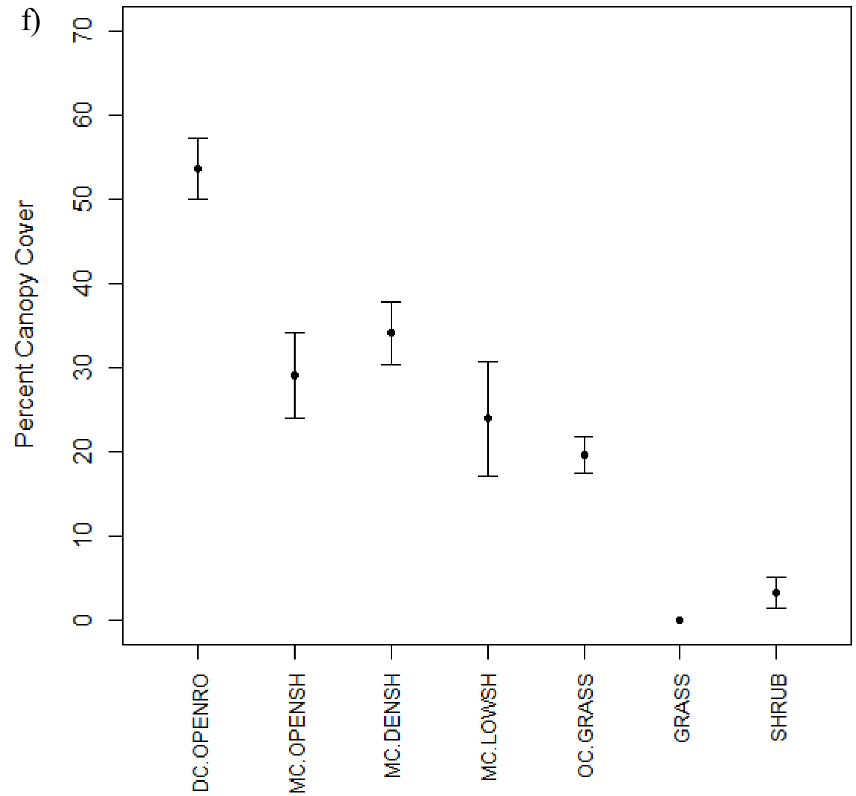
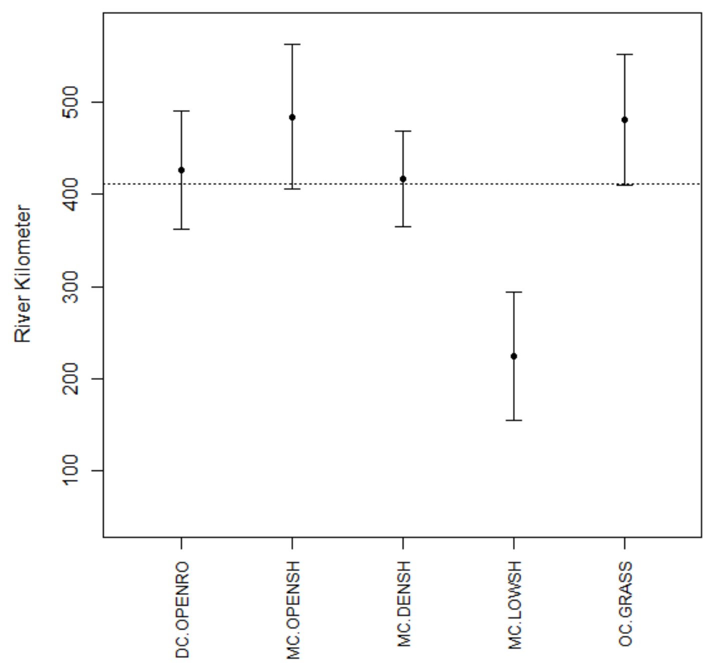


Table 6. Description of vegetation characteristics associated with each habitat type. A positive (+) or negative (--) relationship with a particular vegetation variable indicates higher or lower abundance of that variable within that habitat type compared to other habitats.

Habitat Type	n	Description	Vegetation Variables: Small dbh tree	Large dbh tree	Low native shrub	Tall native shrub	Russian olive	Canopy cover
GRASS	30	No woody stems, only grass and forbs	--	--	--	--	--	--
SHRUB	40	Few trees, lots of variation in number of shrubs, ranging from few to many	--	--				--
DC.OPENRO	56	Dense canopy; open understory with Russian olive	+	+			+	+
MC.OPENSH	37	Moderate canopy; open understory with some native shrub				+		
MC.DENSH	75	Moderate canopy; high density of native shrub			+	+		
MC.LOWSH	30	Moderate canopy; medium density of native shrub that is low to the ground			+			
OC.GRASS	36	Open canopy; few to no shrubs or trees		--				--

Figure 4. Mean river kilometer of sites within cottonwood habitat types. The horizontal dashed line represents the mean river kilometer value of all sites sampled. Error bars represent 95% confidence intervals.



Species Richness

Total species richness differed between cottonwood, shrubland, and grassland habitat types, ranging from an average of 8.06 species at CWFOREST sites (95% CI: 7.82,8.29), to 5.40 species at SHRUB sites (95% CI: 4.69,6.10), to 3.09 species at GRASS sites (95% CI: 2.53,3.65). Trends in NTM species richness were very similar to total species richness, and the number of NTM species ranged from 5.14 at CWFOREST sites (95% CI: 4.95,5.33), to 2.86 at SHRUB sites (95% CI: 2.34,3.37), to 1.83 at GRASS sites (95% CI: 1.39,2.26). Higher species richness at CWFOREST sites is likely due to the greater complexity of vegetation structure and composition compared to the other two habitats (Table 6, Figure 3).

Within cottonwood forest habitat types, total species richness was highest on average at MC.OPENSH and MC.DENSH sites, and lowest at MC.LOWSH and OC.GRASS sites. Richness was slightly lower at DC.OPENRO, although 95% CIs overlapped with all other habitat types (Figure 6). NTM species richness was very similar between DC.OPENRO, MC.OPENSH, and MC.DENSH habitats, and was higher at sites within these habitats than MC.LOWSH and OC.GRASS habitats. However, 95% CIs for MC.OPENSH overlapped with those for MC.LOWSH and OC.GRASS (Figure 6). These results suggest that habitat types with a well-developed overstory but open understory (DC.OPENRO) may support as many total species and NTM species as those cottonwood habitats with a well-developed understory structure but more open canopy cover (MC.OPENSH and MC.DENSH). Furthermore, cottonwood habitats with a structurally simple understory (MC.LOWSH) or canopy (OC.GRASS) may support fewer total species and NTM species than other cottonwood habitats.

Guild richness differed across cottonwood habitats for many of the foraging and nesting guilds. Significant differences in mean richness (i.e. 95% CIs did not overlap for at least two habitat types) were observed for all four of the foraging guilds and two of the four nesting guilds (Table 7). Richness of species that forage in shrubs (FLOW) was highest in MC.DENSH and MC.OPENSH, which are the habitats with the highest densities of tall native shrubs. Similarly, richness of species that nest low in the understory (NLOW) was highest in these two habitats, as well as DC.OPENRO, another habitat with high density of tall shrubs (i.e. Russian olive). Richness of species that forage and nest on the ground (FGND and NGND) were lower in the DC.OPENRO habitat, which has a relatively open understory, and higher in MC.OPENSH, MC.DENSH, and MC.LOWSH, which have the greatest densities of native shrubs. Richness of species that forage in the canopy (FCAN) and in the air (FAIR) were highest in DC.OPENRO, the habitat with a well-developed canopy layer. Richness of species that nest in the canopy (NMSC) and in cavities of trees (NCAV) were relatively constant across all habitats.

The relationship between species richness and river location was examined for each habitat type. Total species richness at cottonwood sites was slightly higher at RKM values near 700 km (435 mi), and lower in the middle reaches and near the mouth. NTM species richness was also higher at high values of RKM (Figure 7a). Both relationships were quadratic in nature, with lower richness at intermediate reaches, and the evidence for these relationships was strong ($p < 0.001$ for total and $p < 0.05$ for NTM richness). The relationship between total richness and RKM in grassland sites was quadratic, but relatively flat ($p = 0.442$; Figure 7b), suggesting that there was little evidence that richness varied across reaches of the river. NTM richness was lower near the mouth of the river (Figure 7b), and this quadratic relationship was significant ($p = 0.047$). However, very few grassland sites were located near the mouth (Figure 7b), suggesting that inference about richness in this segment of the river is limited. Finally, species richness in

Figure 5. Relationships between river kilometer and continuous predictor variables, including a) percent forest cover, b) log distance to crop, and c) log distance to human settlement. General structure of the model and adjusted r^2 values are provided. The solid lines represent predicted values and the dotted lines represent 95% confidence bands on those predictions. Open circles represent actual observations.

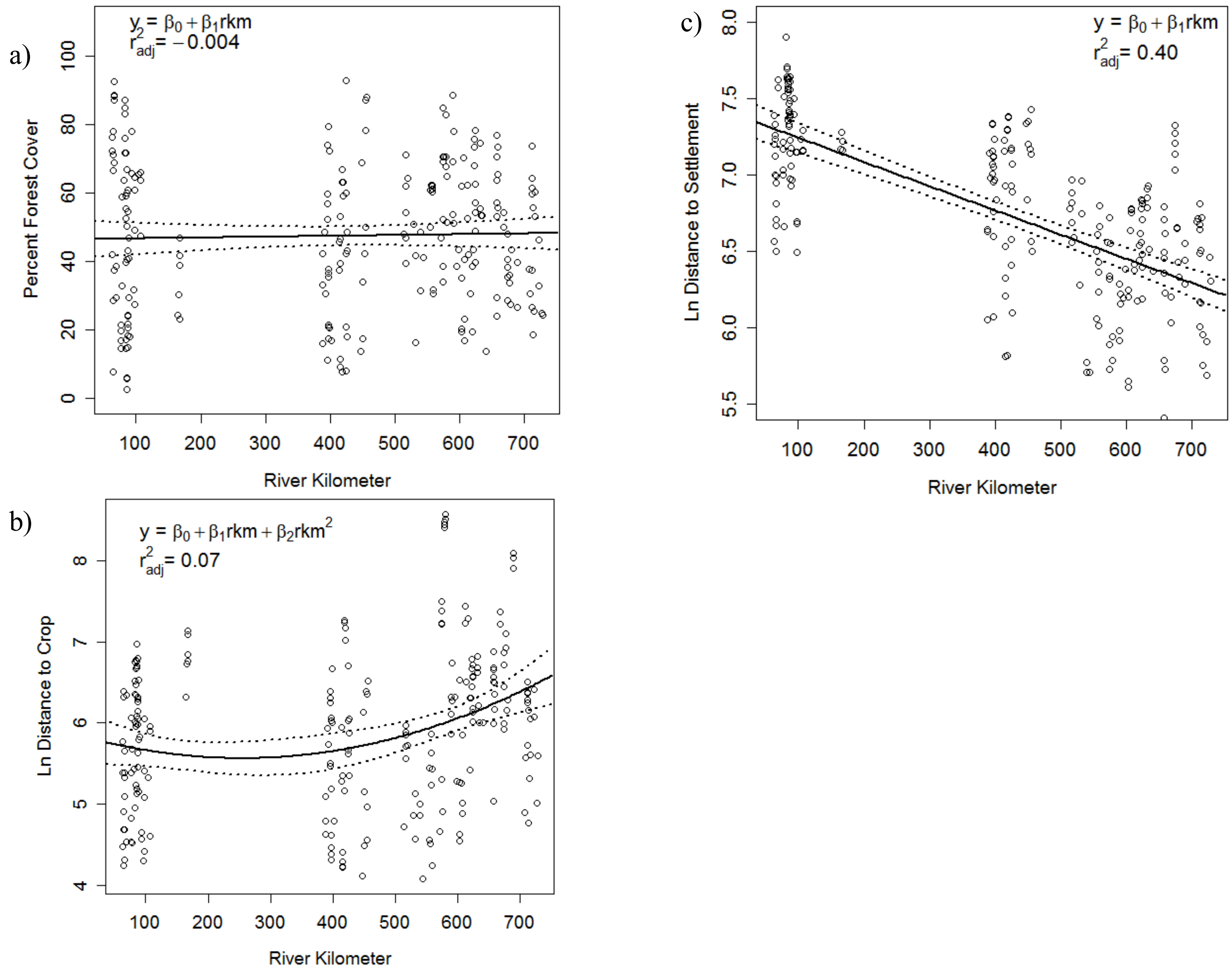


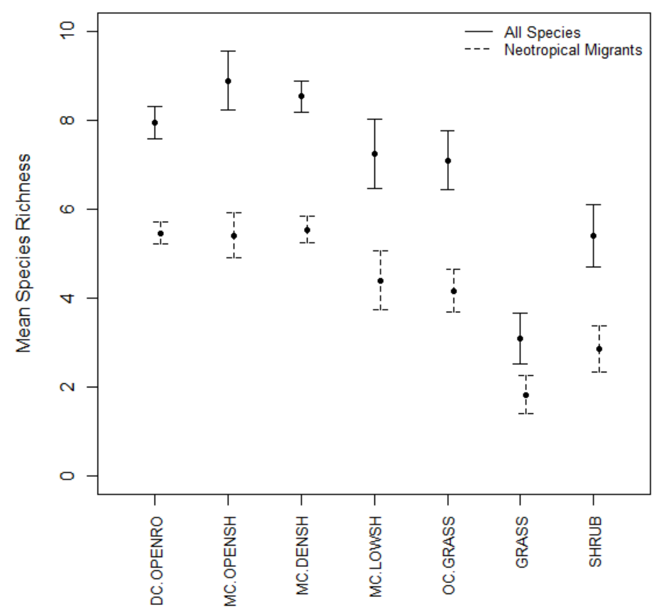
Table 7. Mean species richness of four foraging and four nesting guilds within the five cottonwood habitat types. Mean richness is followed in parentheses by 95% confidence intervals.

	Cottonwood Habitat Type				
Guild	DC. OPENRO	MC. OPENSH	MC. DENSH	MC. LOWSH	OC. GRASS
Foraging[1]					
FGND	1.25 (1.08, 1.42)	1.90 (1.61, 2.20)	1.62 (1.43, 1.80)	1.61 (1.32, 1.90)	1.69 (1.42, 1.97)
FAIR	1.29 (1.10, 1.47)	1.24 (0.97, 1.51)	1.14 (0.97, 1.30)	0.86 (0.63, 1.08)	1.17 (0.89, 1.45)
FLOW	2.67 (2.48, 2.87)	3.55 (3.18, 3.91)	3.61 (3.38, 3.83)	2.79 (2.47, 3.11)	2.68 (2.34, 3.01)
FCAN	2.27 (2.12, 2.42)	1.81 (1.57, 2.06)	1.79 (1.67, 1.91)	1.64 (1.29, 1.99)	1.33 (1.13, 1.53)
Nesting[2]					
NCAV	1.89 (1.71, 2.07)	2.13 (1.85, 2.40)	1.89 (1.71, 2.08)	1.69 (1.37, 2.01)	1.97 (1.68, 2.26)
NGND	0.78 (0.62, 0.94)	1.13 (0.91, 1.35)	1.23 (1.07, 1.38)	1.27 (1.02, 1.53)	0.75 (0.52, 0.99)
NLOW	3.77 (3.57, 3.98)	3.90 (3.44, 4.36)	3.76 (3.50, 4.02)	3.00 (2.54, 3.45)	2.91 (2.49, 3.34)
NMSC	1.12 (0.93, 1.31)	1.21 (0.95, 1.48)	1.08 (0.92, 1.24)	1.04 (0.79, 1.29)	1.00 (0.79, 1.21)

[1] Foraging guilds, by location of foraging activity: FGND = ground, FLOW = ground or shrubs, FCAN = shrubs or canopy, FAIR = on the wing

[2] Nesting guilds, by location of nest: NGND = on/close to ground, NCAV = in cavities, NLOW = shrubs or low canopy, NMSC = midstory or high canopy

Figure 6. Total species richness and richness of Neotropical migrant species within cottonwood (DC.OPENRO, MC.OPENSH, MC.DENSH, MC.LOWSH, and OC.GRASS), grassland (GRASS), and shrubland (SHRUB) habitat types. Points represent mean richness values and error bars represent 95% confidence intervals.



shrubland sites was also generally higher at high RKM values. This relationship was linear for total species richness, but not significant ($p = 0.136$), and quadratic for NTM richness ($p < 0.05$; Figure 7c). However, sample sizes were very small and most shrubland sites were in the eastern reaches of the river, indicating that the strength of inference for shrub sites in the western reaches is limited (Figure 7c).

Relationships between species richness and river location were also examined within cottonwood habitat types. There seemed to be little variation in total or NTM species richness along the river for DC.OPENRO. Relationships were relatively flat (Figure 8a) and were not significant ($p > 0.10$). Total and NTM richness at MC.OPENSH sites were lowest near the mouth of the river, and increased steadily upstream (Figure 8b). These relationships were significant (total and NTM richness $p < 0.001$), and adjusted r^2 values were relatively high (Figure 8b), indicating that much of the variation in species richness was explained by river location. Data for this habitat type were sparse, but were evenly distributed across reaches (Figure 8b). Total richness at MC.DENSH sites was lower at intermediate RKM values, while NTM richness exhibited a slight increase at high RKM (Figure 8c), and these relationships were significant ($p < 0.001$ for total richness and $p < 0.05$ for NTM richness). However, predicted NTM richness was near 6 for all values of RKM (Figure 8c), suggesting that the differences in the number of NTM species were relatively small across reaches even though results were significant. River location had little effect on total or NTM species richness at MC.LOWSH sites; relationships were relatively flat and were not significant ($p > 0.20$ for both; Figure 8d). Few sites were located in the western region (Figure 8d), so inference was not strong in this section of the river for this habitat type. Finally, total and NTM richness was lower near the mouth of the river and increased upstream at OC.GRASS sites (Figure 8e). These relationships were significant ($p < 0.05$ for total and $p < 0.001$ for NTM richness). Adjusted r^2 values were also high, suggesting that river location explained a moderate amount of the variation in species richness. However, data for this habitat type was very sparse in many reaches (Figure 8e).

Bird Occupancy and Abundance

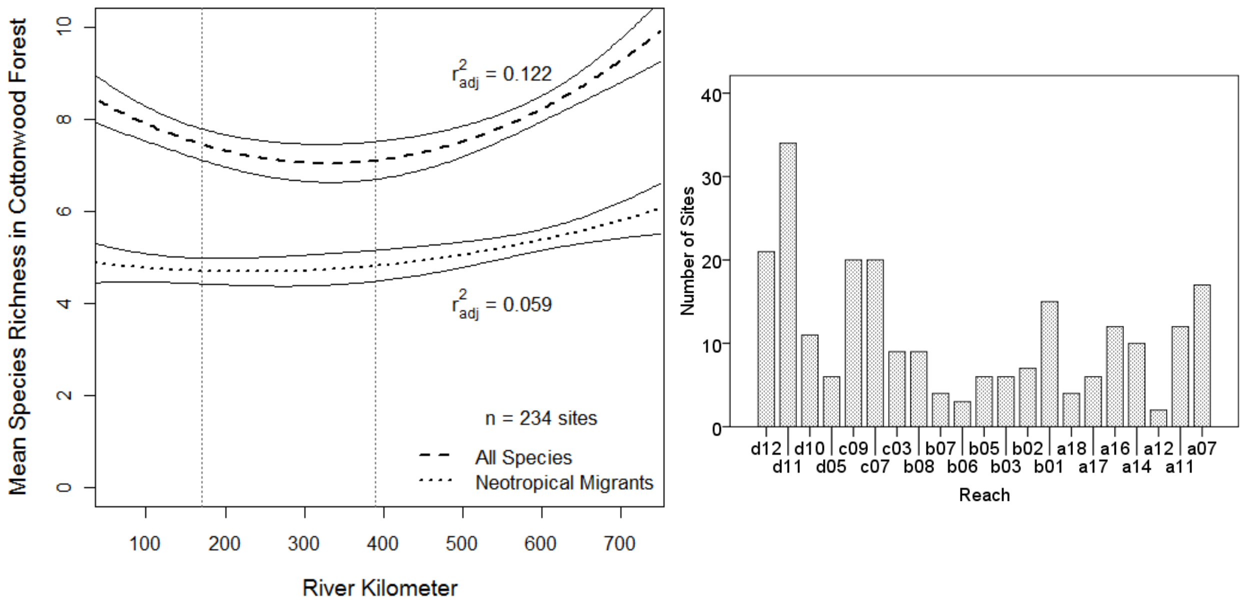
Excluding non-target species (i.e. ducks, raptors, shorebirds, and upland gamebirds), 64 species of birds were observed at 234 cottonwood forest sites over the two years (Appendix 1). Yellow warbler (99.6% of sites), House wren (96.6%), Northern flicker (80.3%), Brown-headed cowbird (74.4%), and Yellow-breasted chat (73.5%) were the most common species. 182 sites were surveyed in 2006 and 232 in 2007; all but two of the sites surveyed in 2006 were surveyed again in 2007. Fourteen species were included in occupancy and abundance analysis (Table 3).

Habitat type was included in top-ranking models for nine species (Table 8). This was consistent with the expectation that local habitat characteristics would be an important influence on ψ or abundance for most of the species. Habitat was not included in top-ranking models for ovenbirds, which we had expected based on their strong affinity for dense, contiguous forest, which is a limited resource in riparian zones and a potentially more important factor driving occupancy. However, habitat was included in top-ranking models for European starlings when we had expected that local habitat characteristics would not be important for this species.

Many of the species for which habitat was included in top-ranking models exhibited trends of higher or lower occupancy rates in at least one of the five habitat types. Guild associations were generally good predictors of preferred habitat types for each species. For example, species that nested and foraged low in the understory were found more often and at

Figure 7. Predicted species richness along the river within each of three main habitat types, including a) cottonwood forest, b) grassland, and c) shrubland. Both total species richness and richness of NTM species are included. Solid lines bordering broken lines represent 95% confidence bands on predicted richness. The area between the two vertical dotted gray lines identifies river kilometer values within the region of 'no data', where surveys were not conducted (i.e. between river km 170 and 390). Bar graphs adjacent to the line graph show the sample sizes within reaches of the river for that habitat type. Reaches are ordered from east to west to coincide with river kilometer values on the line graph (i.e. 0 is the mouth of the river, the eastern-most point of the study area, and d12 is the eastern-most reach).

a)



b)

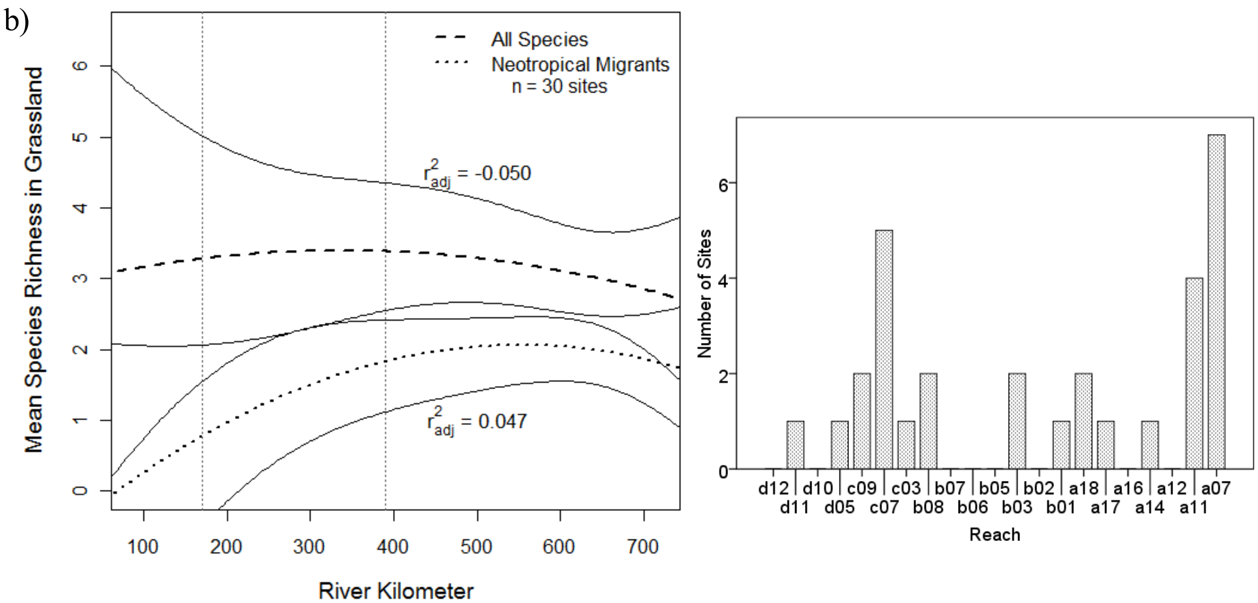
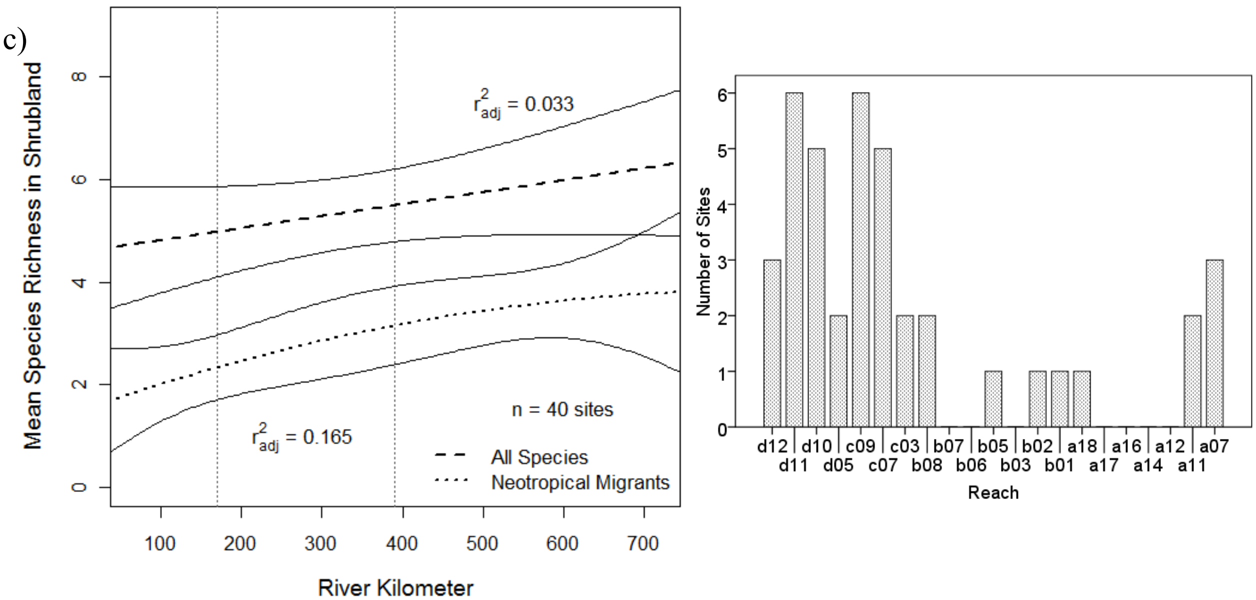


Figure 7 continued.

c)

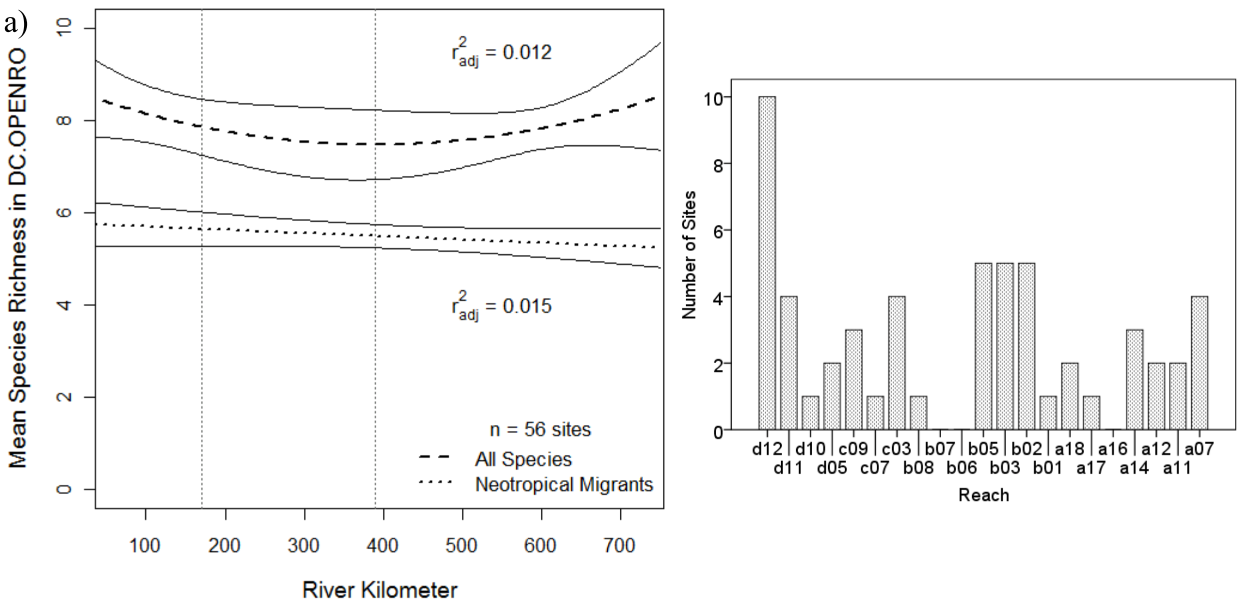


higher abundance in the habitat type with the densest shrub layer (MC.DENSH), while species that foraged and nested higher in the canopy seemed to prefer the habitat type with highest canopy cover (DC.OPENRO). A few species shared membership in the same nesting and foraging guilds (Table 3), and these species generally preferred the same habitat types. Five species had high probability of occupancy or abundance in the DC.OPENRO habitat type compared with other habitat types, while three and six species (respectively) were found at higher occupancy or abundance in the MC.OPENSH and the MC.DENSH habitats. Only one species seemed to prefer each of the MC.LOWSH and OC.GRASS habitats, while many species were found at lower occupancy or abundance in these habitat types. Many species experienced high occupancy rates and abundance in multiple habitats, and few species seemed to prefer a single habitat type.

Percent forest cover surrounding a site was an important predictor of ψ or abundance for more than 70% (10 of 14) of species (Table 8). When forest cover was included in top-ranking models, it often received a high cumulative model weight ($\sum w_i \geq 0.89$ for all ten species; Table 9), indicating that it was an influential variable compared with other variables. Four species responded negatively to forest cover while six responded positively (Table 10). Results were consistent with expectations in most cases (Table 3). However, three species showed a positive response to forest cover when a negative response was expected. In all cases, relationships with the main effect of forest cover were significant at the 95% confidence level in at least one year (Table 10).

Figure 8. Predicted species richness within cottonwood habitat types, including a) DC.OPENRO, b) MC.OPENSH, c) MC.DENSH, d) MC.LOWSH, and e) OC.GRASS. Dashed lines represent predicted values of total species richness, while dotted lines represent predicted NTM richness. Solid lines bordering broken lines are 95% confidence bands on predicted richness. The area between the two vertical dotted gray lines identifies river kilometer values within the region of 'no data', where surveys were not conducted (i.e. between river km 170 and 390). Bar graphs adjacent to the line graph show the sample sizes within reaches of the river for that habitat type. Reaches are ordered from east to west to coincide with river kilometer values on the line graph (i.e. 0 is the mouth of the river, the eastern-most point of the study area, and d12 is the eastern-most reach).

a)



b)

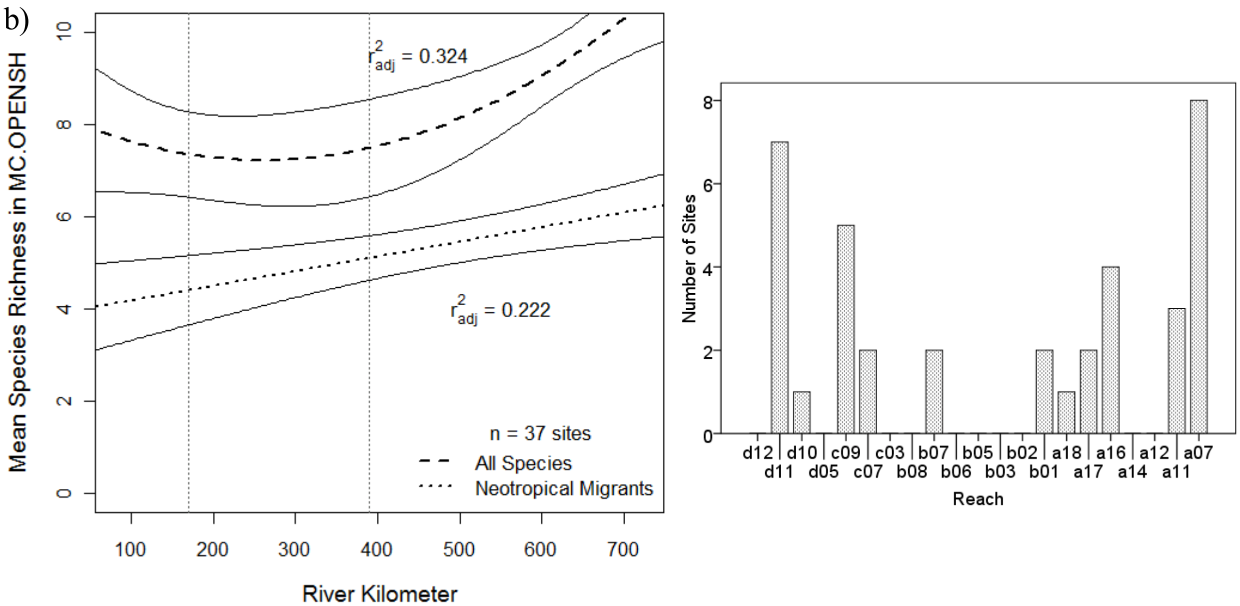
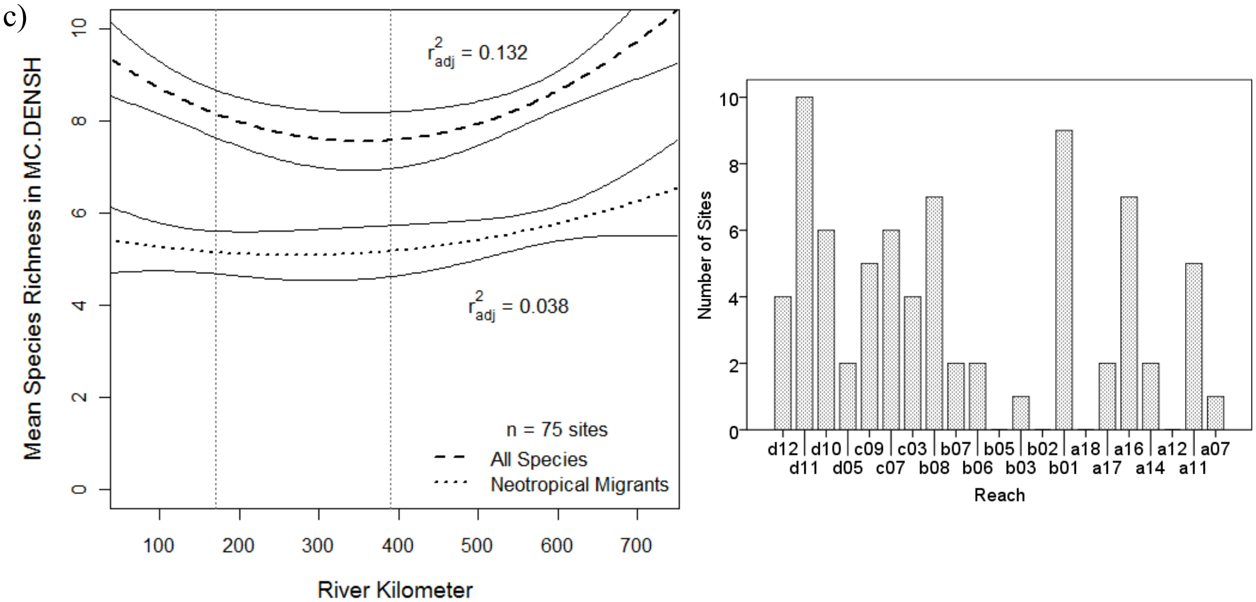


Figure 8 continued.

c)



d)

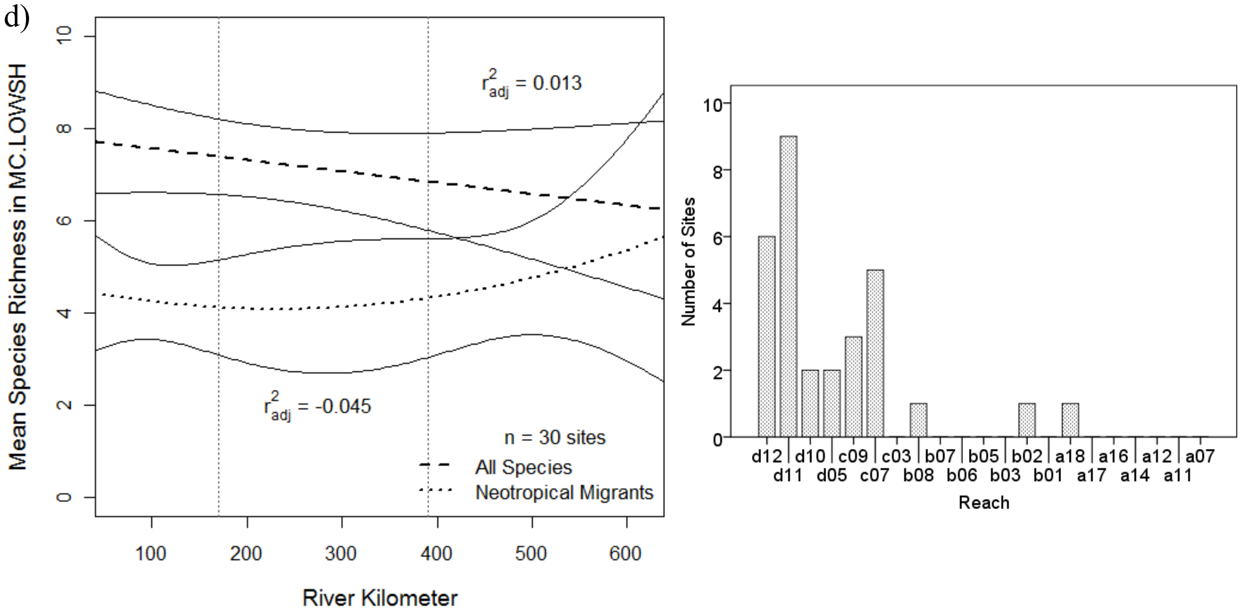
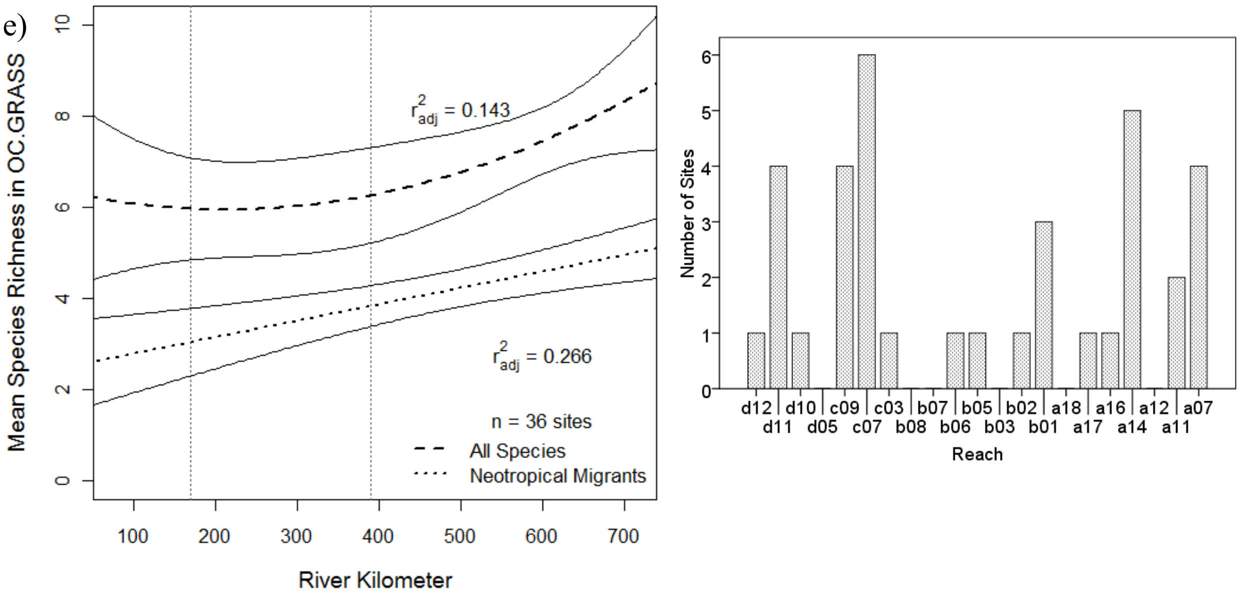


Figure 8 continued.

e)



Log distance to the nearest irrigated crop field was included in top-ranking models for seven species (Table 8). For all but one species, the main effect was negative, suggesting a positive association with agricultural fields (Table 10). Results were generally consistent across years for all species, and the main effect of LNCROP was significant or marginally significant at the 95% confidence level for four of the seven species, while the quadratic effect was significant for one (Table 10). However, cumulative weights of models that included LNCROP were low for most species ($\sum w_i \leq 0.40$ for eleven species; Table 9), indicating that this variable was not highly influential compared to the other predictor variables.

Log distance to settlement was included in top-ranking models for 12 species (Table 8). For three species, the main effect of distance to settlement was positive (i.e. a negative association with sites located nearer to settlement), but this was significant at the 95% confidence level for only one species. For six species, the main effect was negative, but was significant at the 95% confidence level for only two species. For two species, there was evidence for a significant quadratic effect. Trends were consistent across years for all species except ovenbirds and common yellowthroats (Table 10). For two of the species with observed positive relationships, expected relationships were also positive. For one species, a negative relationship was both expected and observed (Table 3). Cumulative weights for LNSETT were low for half of the species ($\sum w_i < 0.40$; Table 9), suggesting that distance to settlement was not one of the most important predictor variables for these species.

Table 8. Top-ranking occupancy and abundance models for each species, as determined using AIC model selection methods. A model is considered 'top-ranking' if it is within 2 AICc or QAICc units (i.e. Δ(Q)AICc $\leq$ 2.0) of the model with the lowest score. See 'Methods' for a description of predictor variables included in models. AICc and QAICc weights (w_i) represent the weight of the evidence for a particular model given the data.

Species	Top-ranking ψ or Abundance Models(s)	Δ (Q)AICc	(Q)AICc w_i
Common Yellowthroat	FCOV+RKM+RKM^2	0	0.42
	FCOV+LNSETT+LNSETT^2+RKM+RKM^2	0.87	0.27
	FCOV+LNCROP+LNCROP^2+RKM+RKM^2	1.89	0.16
European Starling	LNSETT+LNSETT^2+RKM+RKM^2	0	0.34
	HAB+ LNSETT+LNSETT^2+RKM+RKM^2	0.60	0.25
	HAB+RKM+RKM^2	1.70	0.15
Gray Catbird	HAB+FCOV+RKM+RKM^2	0	0.22
	HAB+FCOV+LNSETT+LNSETT^2+RKM+RKM^2	0.07	0.22
	HAB+FCOV+LNCROP+LNCROP^2+RKM+RKM^2	0.34	0.19
	FCOV+RKM+RKM^2	0.49	0.17
	FCOV+LNCROP+LNCROP^2+RKM+RKM^2	1.83	0.09
Least Flycatcher	HAB+FCOV+LNCROP+LNCROP^2+RKM+RKM^2	0	0.99
Ovenbird	FCOV+FCOV^2+RKM	0	0.54
	FCOV+FCOV^2+LNSETT+RKM	1.46	0.26
Red-eyed Vireo	HAB+RKM	0	0.46
Song Sparrow	HAB+FCOV+FCOV^2+LNSETT+RKM +RKM^2	0	0.66
Spotted Towhee	RKM+RKM^2	0	0.36
	LNSETT+LNSETT^2+RKM+RKM^2	1.02	0.22
Warbling Vireo	HAB+FCOV+LNSETT+LNCROP +RKM	0	0.38
	HAB+FCOV+LNSETT+LNCROP	1.94	0.14
Western Wood-pewee	FCOV+LNSETT+LNSETT^2+RKM+RKM^2	0	0.61
	FCOV+LNSETT+LNSETT^2+LNCROP+LNCROP^2 +RKM+RKM^2	1.28	0.32
Yellow-breasted Chat	HAB+LNSETT+RKM+RKM^2	0	0.52
Yellow Warbler	HAB+FCOV+FCOV^2+LNCROP+RKM+YR	0	0.57
	HAB+FCOV+FCOV^2+LNSETT+LNCROP+RKM+YR	1.13	0.32
House Wren	HAB+FCOV+FCOV^2+LNSETT+LNSETT^2+RKM+YR	0	0.83
Brown-headed Cowbird	FCOV+LNSETT+RKM+RKM^2+YR	0	0.45
	FCOV+LNSETT+LNCROP+RKM+RKM^2+YR	1.21	0.24

River location was included in top-ranking models of ψ or abundance for all species (Table 8). Nine species exhibited a positive relationship with RKM, indicating that ψ or abundance was higher in the western reaches of the study area for those species. Five species were negatively associated with RKM. Trends were very consistent across years, and either the main or quadratic effects of RKM were significant at the 95% confidence level for all but one species (Table 10).

Detailed results are discussed below for each species. See Appendix 4 for a summary of relationships between bird community characteristics and environmental variables.

Table 9. Cumulative model weights for each predictor variable for each species included in occupancy and abundance analysis. Cumulative model weights ($\sum w_i$) are the sum of the AICc or QAICc weights of all models in the candidate model set that include a particular variable. A variable that is included in many of the top-ranking models will have a $\sum w_i$ close to 1.0. Results are reported as the sum of the weights of the top-ranking models that include a variable, followed in parentheses by the sum of the weights of all models with a weight of at least 0.01 that include the variable. See 'Methods' for a description of the predictor variables used in analysis.

	(Q)AICc Cumulative Weight ($\sum w_i$)				
Species	HAB	FCOV$^{(2)}$	LNSETT$^{(2)}$	LNCROP$^{(2)}$	RKM$^{(2)}$
Common Yellowthroat	0 (0.10)	0.85 (0.99)	0.27 (0.34)	0.16 (0.22)	0.85 (0.99)
European Starling	0.40 (0.46)	0 (0.05)	0.59 (0.65)	0 (0.06)	0.74 (0.98)
Gray Catbird	0.63 (0.66)	0.89 (0.98)	0.22 (0.31)	0.28 (0.32)	0.89 (0.98)
Least Flycatcher	0.99 (0.99)	0.99 (0.99)	0 (0)	0.99 (0.99)	0.99 (0.99)
Ovenbird	0 (0.08)	0.80 (0.99)	0.26 (0.31)	0 (0.11)	0.80 (0.99)
Red-eyed Vireo	0.46 (0.97)	0 (0.15)	0 (0.24)	0 (0.24)	0.46 (0.97)
Song Sparrow	0.66 (0.97)	0.66 (0.99)	0.66 (0.69)	0 (0.08)	0.66 (0.99)
Spotted Towhee	0 (0.19)	0 (0.18)	0.22 (0.32)	0 (0.09)	0.58 (0.96)
Warbling Vireo	0.52 (0.94)	0.52 (0.91)	0.52 (0.74)	0.52 (0.68)	0.38 (0.51)
Western Wood-pewee	0 (0.04)	0.93 (1.00)	0.93 (0.97)	0.32 (0.36)	0.93 (1.00)
Yellow-breasted Chat	0.52 (0.94)	0 (0.23)	0.52 (0.78)	0 (0.10)	0.52 (0.94)
Yellow Warbler	0.89 (0.99)	0.89 (0.89)	0.32 (0.36)	0.89 (0.99)	0.89 (0.99)
House Wren	0.83 (0.95)	0.83 (0.99)	0.83 (0.99)	0 (0.14)	0.83 (0.99)
Brown-headed Cowbird	--	0.69 (0.96)	0.69 (0.89)	0.24 (0.40)	0.69 (0.99)

Common Yellowthroat. Common yellowthroats (*Geothlypis trichas*) were observed at 58% of cottonwood sites in at least one of the two years (Appendix 1); 43% of sites in 2006 and 50% in 2007. FCOV, LNCROP, LNCROP^2, LNSETT, LNSETT^2, RKM, and RKM^2 were included in top-ranking models for ψ (Table 8). Occupancy was negatively related to FCOV (Table 10, Figure 9a), which was consistent with expectations for this species (Table 3). Occupancy was positively associated with LNCROP, although we had predicted that yellowthroats would show a negative response (Table 3). However, confidence intervals overlapped zero in all cases (Table 10), and cumulative AICc weights for this variable were low (($\sum w_i$ = 0.34; Table 9), suggesting a lack of strong evidence for the effect of LNCROP. Finally, there was strong evidence that yellowthroats had a negative association with RKM, indicating that occupancy rates were higher in the eastern reaches of the study area, near the mouth of the river (Table 10, Figure 10a). FCOV and RKM seemed to have the strongest influence on yellowthroat occupancy, as all top-ranking models included these variables (Table 8), and cumulative model weights were very high (Table 9).

Yellowthroats were expected to respond positively to LNSETT, but the data suggested that this variable actually had little influence on ψ (Table 9). Habitat type was also not included in top-ranking models, suggesting that this was not an influential variable compared with other predictor variables. Additionally, cumulative model weight was very low for this variable (Table 9). Guild membership (Table 3) predicted that yellowthroats would prefer a semi-open understory for nesting on the ground, but a dense understory and low canopy for foraging. These contrasting habitat requirements may indicate that yellowthroats are not restricted to any one particular cottonwood habitat. Yellowthroats shared foraging and nesting guild associations with spotted towhees (Table 3), a species for which habitat type was also not an influential variable (Table 8, Table 9).

Table 10. Estimates and 95% confidence intervals (in parentheses) of parameters for variables included in top-ranking occupancy and abundance regression models. Top-ranking models include those within 2 units of the model with the lowest AICc or QAICc score. See Table 9 for a list of top-ranking models for each species. If a variable was included in more than one top-ranking model, results for that variable are reported from the highest-ranking model (i.e. with the lowest AICc or QAICc score). Data are reported for each year for all continuous predictor variables.

Species	Year	Predictor Variable							
		FCOV	$FCOV^2$ (x e-4*)	LNSETT	$LNSETT^2$	LNCROP	$LNCROP^2$	RKM (x e-2*)	RKM^2 (x e-5*)
Common Yellowthroat	2006	-0.062 (-0.138,0.014)		-0.73 (-2.49,1.02)	0.28 (-0.88,1.44)	0.56 (-0.38,1.50)	0.04 (-0.47,0.55)	-0.8 (-1.4,-0.2)	-1.6 (-4.0,0.73)
	2007	-0.048 (-0.082,-0.014)		0.40 (-0.97,1.78)	1.15 (-0.36,2.66)	0.11 (-0.62,0.84)	0.40 (-0.14,0.94)	-0.4 (-0.7,-0.1)	-0.02 (-1.6,1.6)
European Starling	2006			0.51 (-0.61,1.63)	0.03 (-0.90,0.95)			0.9 (0.3,1.4)	1.7 (-0.3,3.7)
	2007			0.70 (-0.26,1.67)	-0.81 (-1.82,0.20)			0.6 (0.3,1.0)	2.2 (0.9,3.47)
Gray Catbird	2006	-0.035 (-0.065,-0.005)		-0.46 (-1.83,0.91)		-0.08 (-0.82,0.66)	0.42 (-0.21,1.05)	0.9 (0.2,1.5)	2.0 (-0.4,5.0)
	2007	-0.035 (-0.060,-0.011)		-1.04 (-2.20,0.11)		-0.36 (-0.97,0.25)	0.48 (0.06,0.90)	0.6 (0.3,0.9)	2.0 (0.2,3.0)
Least Flycatcher	2006	0.037 (0.017,0.057)				-0.80 (-1.34,-0.27)	-0.67 (-1.13,-0.23)	0.3 (0.05,0.5)	1.0 (-0.2,2.0)
	2007	0.044 (0.025,0.064)				-0.82 (-1.26,-0.39)	-0.17 (-0.47,0.13)	0.3 (0.1,0.5)	2.0 (0.5,3.0)
Ovenbird	2006	0.031 (0.008,0.053)	4.0 (-5.0,14.0)	-0.70 (-1.66,0.26)				-0.2 (-0.4,-0.08)	
	2007	0.038 (0.012,0.064)	10.0 (0.5,19.0)	0.53 (-0.59,1.65)				-0.6 (-0.9,-0.3)	
Red-eyed Vireo	2007							-0.5 (-0.7,-0.3)	
Song Sparrow	2006	-0.072 (-0.108,-0.037)	-12.0 (26.0,3.0)	-0.91 (-2.07,0.26)				0.4 (-0.003,0.8)	-2.0 (-4.0,-1.0)
	2007	-0.017 (-0.038,0.004)	5.0 (-5.0,14.0)	-0.88 (-1.80,0.05)				0.2 (-0.08,0.5)	-1.0 (-2.0,0.3)
Spotted Towhee	2006			-1.31 (-2.92,0.31)	-1.16 (-2.41,0.09)			-0.8 (-1.1,-0.5)	-3.0 (-5.0,-1.0)
	2007			-2.89 (-7.02,1.24)	-1.30 (-3.53,0.94)			-3.1 (-8.0,1.9)	4.0 (-9.0,20.0)

Species	Year	Predictor Variable							
		FCOV	$FCOV^2$ (x e-4*)	LNSETT	$LNSETT^2$	LNCROP	$LNCROP^2$	RKM (x e-2*)	RKM^2 (x e-5*)
Warbling Vireo	2006	0.041 (0.010,0.072)		1.55 (0.17,2.94)		-0.80 (-1.66,0.05)		0.4 (-0.04,0.8)	
Western Wood-pewee	2006	0.059 (0.028,0.089)		0.30 (-0.94,1.54)	-1.43 (-2.62,-0.23)	-0.62 (-1.19,-0.05)	-0.12 (-0.53,0.29)	0.7 (0.02,1.3)	1.0 (-1.0,3.0)
	2007	0.034 (0.015,0.052)		0.78 (-0.16,1.73)	-0.50 (-1.27,0.26)	-0.27 (-0.74,0.19)	0.19 (-0.18,0.57)	0.6 (0.3,0.9)	2.0 (0.3,3.0)
Yellow-breasted Chat	2006			-1.48 (-2.87,-0.08)				-0.6 (-1.0,-0.01)	-3.0 (-5.0,-1.0)
Yellow Warbler	--	0.005 (0.0004,0.010)	-1.0 (-3.0,1.0)	-0.09 (-0.30,0.12)		-0.16 (-0.27,-0.05)		0.3 (0.2,0.4)	
House Wren	--	0.023 (0.018,0.028)	-2.0 (-4.0,0.4)	0.28 (-0.04, 0.60)	-0.35 (-0.58,-0.12)			0.2 (0.1,0.3)	
Brown-headed Cowbird	--	-0.005 (-0.009,-0.002)		-0.20 (-0.38,-0.01)		-0.06 (-0.16,0.04)		0.1 (0.03,0.2)	0.3 (0.02,0.6)

*all numbers for these variables are reported in scientific notation.

Figure 9. Effect of percent forest cover on the occupancy (ψ) or abundance of ten species of birds, including a) common yellowthroat, gray catbird, and song sparrow, b) least flycatcher, ovenbird, warbling vireo, and western wood-pewee, and c) house wren, yellow warbler, and brown-headed cowbird. Occupancy or abundance was estimated using the highest ranking model that included forest cover for each species. Parameter estimates from 2007 were used unless estimates were not available for that year, then 2006 estimates were used. All other variables included in the model were held constant at their mean values, except for the categorical variable HAB, which was held constant at habitat type 'DC.OPENRO'. Points and error bars on the lines of predicted occupancy rate (ψ) represent estimated occupancy and 95% confidence intervals at the approximate 1st and 3rd quartiles for forest cover. Gray lines bordering black lines of predicted abundance represent 95% confidence bands on those predicted values.

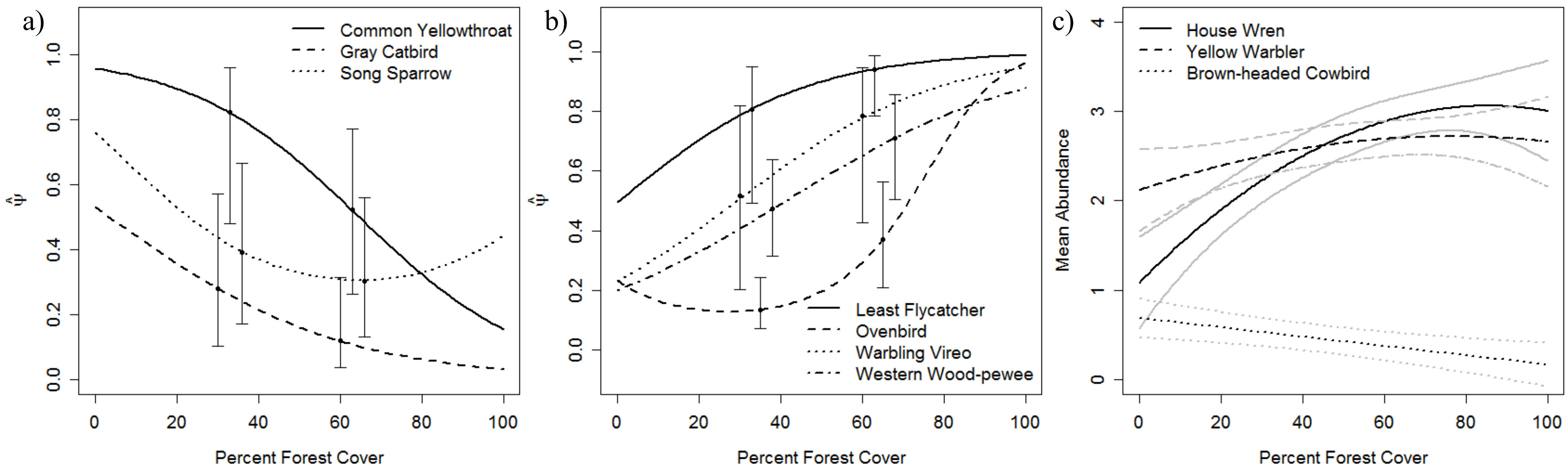
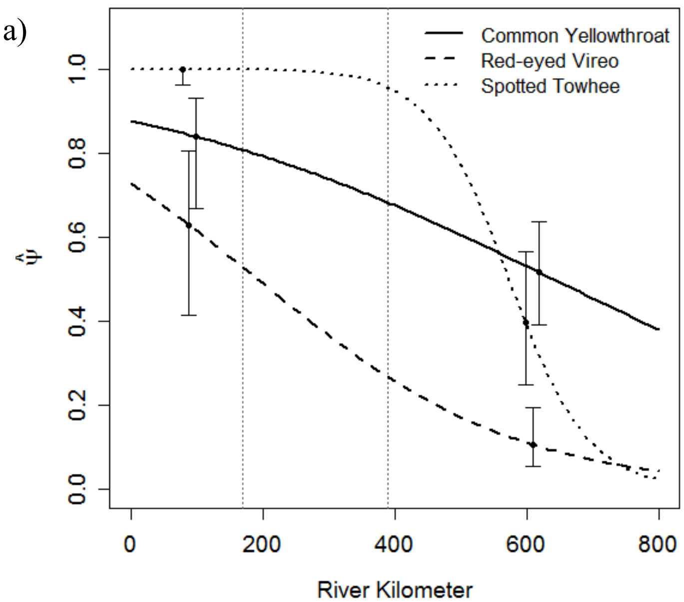


Figure 10. Effect of river kilometer on the occupancy or abundance of 13 species of birds, including a) common yellowthroat, red-eyed vireo, and spotted towhee, b) European starling, song sparrow, and western wood-pewee, c) gray catbird, least flycatcher, ovenbird, and yellow-breasted chat, and d) yellow warbler, house wren, and brown-headed cowbird. Occupancy or abundance was estimated using the highest ranking model that included river kilometer for each species. Parameter estimates from 2007 were used unless estimates were not available for that year, then 2006 estimates were used. All other variables included in the model were held constant at their mean values, except for the categorical variable HAB, which was held constant at habitat type 'DC.OPENRO'. Points and error bars on the lines of predicted occupancy rate (ψ) represent estimated occupancy and 95% confidence intervals at the approximate 1st and 3rd quartile values for river kilometer. Gray lines bordering black lines of predicted abundance represent 95% confidence bands on those predicted values. Values of river kilometer that are in between the two vertical dotted gray lines identify the region of 'no data' where surveys were not conducted.

a)



b)

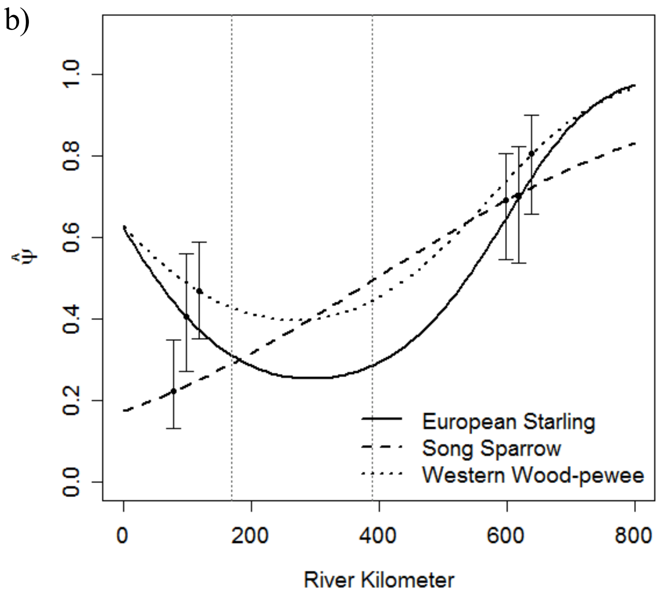
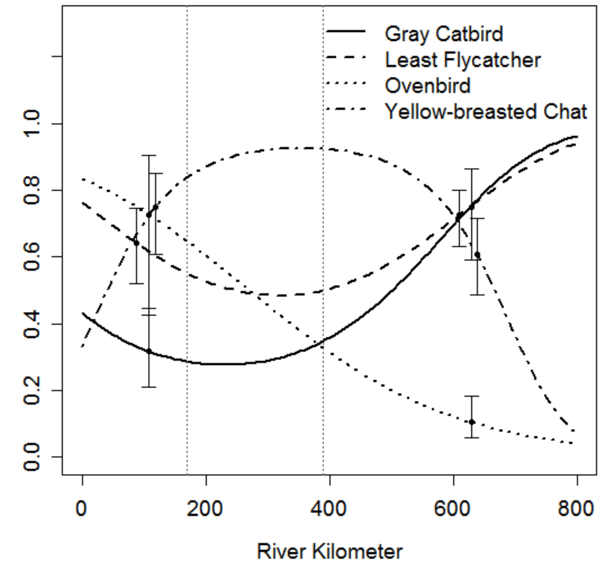
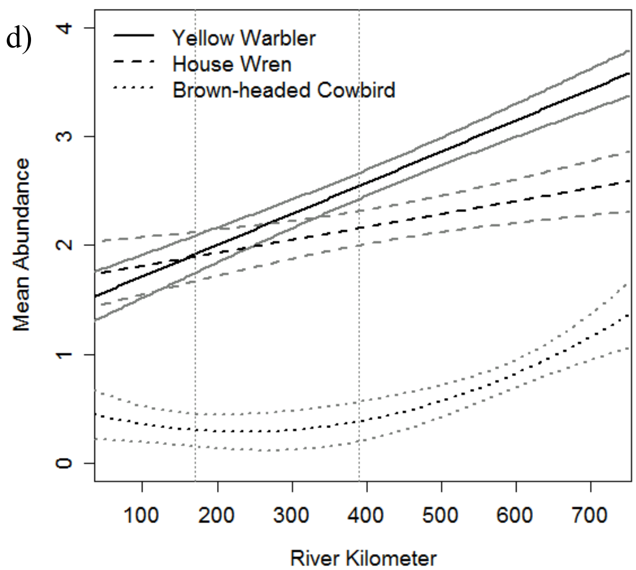


Figure 10 continued.

c)



d)



<u>European Starling</u>. European starlings (*Sturnus vulgaris*) were observed at 53% of cottonwood sites in at least one of the two years (Appendix 1), 41% of site in each of 2006 and 2007. HAB, LNSETT, LNSETT^2, RKM, and RKM^2 were included in top-ranking ψ models (Table 8). Habitat type was included in two of the three top-ranking models, which was contrary to the expectation that HAB would not be important to starling occupancy rates. However, cumulative model weights were not high ($\sum w_i < 0.50$; Table 9), suggesting that habitat was not one of the most influential predictor variables. Estimated ψ within cottonwood habitats was relatively constant across all five habitat types in 2007, but was slightly lower in the MC.LOWSH in 2006 when compared with the other shrub habitats (MC.OPENSH and MC.DENSH; Figure 11a). Foraging and nesting guild associations do not seem to be an important predictor of occupancy within habitat types for starlings. They nest in cavities that are

most commonly found in bigger, older trees which were observed at high abundances in mature cottonwood forests of all types (Figure 3b). Furthermore, starlings will travel relatively far distances to forage, so foraging requirements may not restrict them to a particular breeding habitat type.

Occupancy rates were positively related to LNSETT, which was consistent with predictions for this species (Table 3). However, 95% CIs overlapped zero suggesting a lack of strong evidence for this relationship (Table 10). Furthermore, cumulative model weights for LNSETT were relatively low ($\sum w_i < 0.50$; Table 9), suggesting that LNSETT was not one of the most influential predictor variables. There was strong evidence for a positive, quadratic relationship between ψ and RKM, with starlings having lowest ψ at intermediate reaches, and highest ψ in western reaches farthest from the mouth of the river (Table 10, Figure 10b). All top-ranking models included river location (Table 8), and cumulative model weights were very high for RKM ($\sum w_i = 0.98$; Table 9). There was no support for the expectation that starlings would respond negatively to percent forest cover (Table 3), as this variable was not included in top-ranking models (Table 8), and cumulative model weights were essentially zero (Table 9).

<u>Gray Catbird</u>. Gray catbirds (*Dumetella carolinensis*) were observed at 55% of cottonwood sites in at least one of the two years (Appendix 1); 45% of sites in 2006 and 42% in 2007. All variables were included in top-ranking models of ψ (Table 8). HAB was included in three of the five top-ranking models (Table 8), and cumulative model weight was 0.66 (Table 10), suggesting that local habitat was relatively important to ψ. Estimated ψ was generally higher in the habitats with tall native shrub (MC.OPENSH and MC.DENSH), and this pattern was more evident in 2007 than in 2006 (Figure 11b). Guild membership predicts that catbirds would prefer habitats with a well-developed shrub understory (Table 3), and this is supported by these results. Catbirds are less likely to occur in the MC.LOWSH habitat type than the other two shrub habitats, possibly because the shrubs in this habitat are much lower to the ground (Table 6, Figure 3c), and would not provide the complex understory structure needed for nesting and foraging. Catbirds share foraging and nesting guild associations with yellow-breasted chats (Table 3), a species that also was more likely to occupy the MC.DENSH habitat type.

Occupancy rates were negatively related to FCOV (Table 10, Figure 9a), which was consistent with the expectation for this edge-habitat species (Table 3). The evidence for this relationship was strong, as FCOV was included in all top-ranking models (Table 8), cumulative weight was high (($\sum w_i = 0.99$; Table 9), and 95% CIs for parameter estimates did not overlap zero (Table 10). There was weak evidence for a negative relationship between ψ and distance to crop, but stronger evidence for a positive quadratic relationship, with lowest ψ at intermediate values of LNCROP (Table 10, Figure 8a). High ψ at higher and lower values of LNCROP may reflect the affinity of this species for edge habitats. Edge habitat is more abundant when crop fields border riparian forest because fields create an abrupt, continuous edge. However, edge habitat may also be more abundant where crops are farthest away from the riparian zone because the floodplain is generally smaller in areas that are less suitable for crop production. Riparian forests in these areas may also be smaller, with more available edge habitat. A negative effect of LNSETT was included in one of the top-ranking models (Table 8), but the evidence for this relationship was weak, as 95% CIs overlapped zero in both years (Table 10). Finally, there was strong evidence for a positive, quadratic relationship between ψ and RKM, suggesting that catbirds were more likely to occupy sites in the western region of the study area (Table 10, Figure 10c).

Figure 11. Estimated probability of occupancy (ψ) or mean abundance within cottonwood habitat types for nine bird species, including a) European starling, b) gray catbird, c) least flycatcher, d) red-eyed vireo, e) song sparrow, f) warbling vireo, g) yellow-breasted chat, h) yellow warbler, and i) brown-headed cowbird. Naïve occupancy is the percentage of sites occupied for each habitat type, uncorrected for imperfect detection. Points represent estimated ψ or mean abundance and bars represent 95% confidence intervals. Results are presented for both 2006 (solid lines) and 2007 (dashed lines) for most species. Only one year is presented for red-eyed vireo, warbling vireo, and yellow-breasted chat due to problems with convergence of models in the missing year.

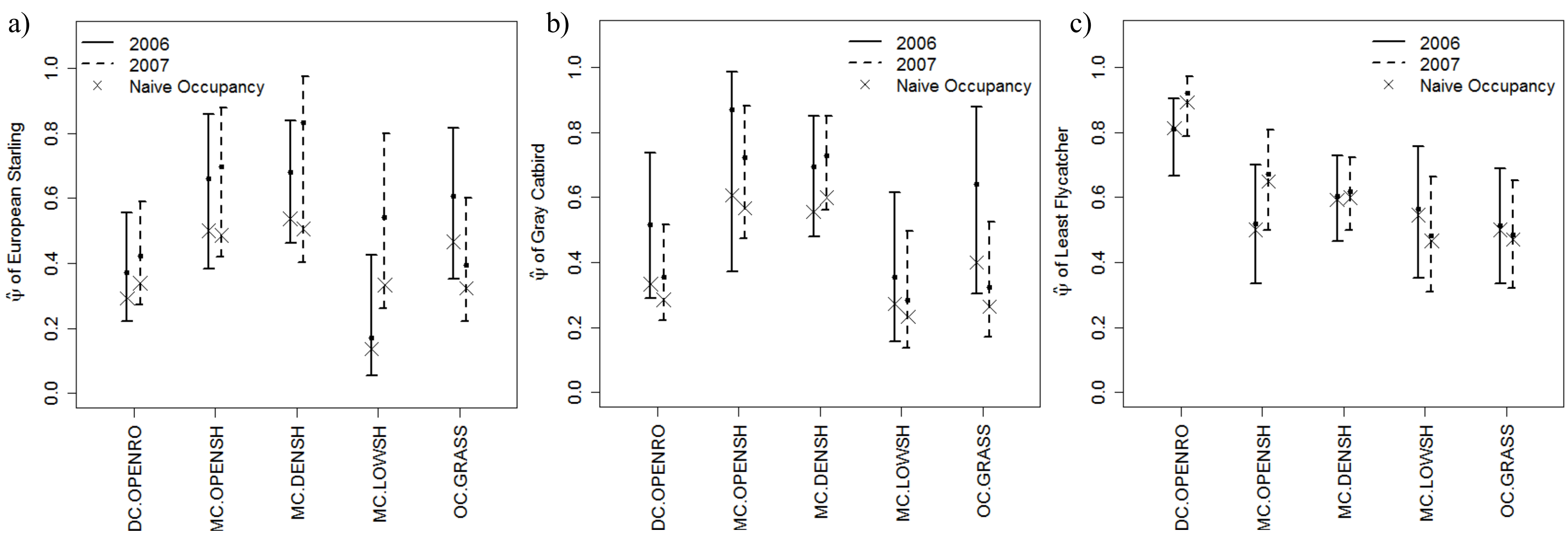
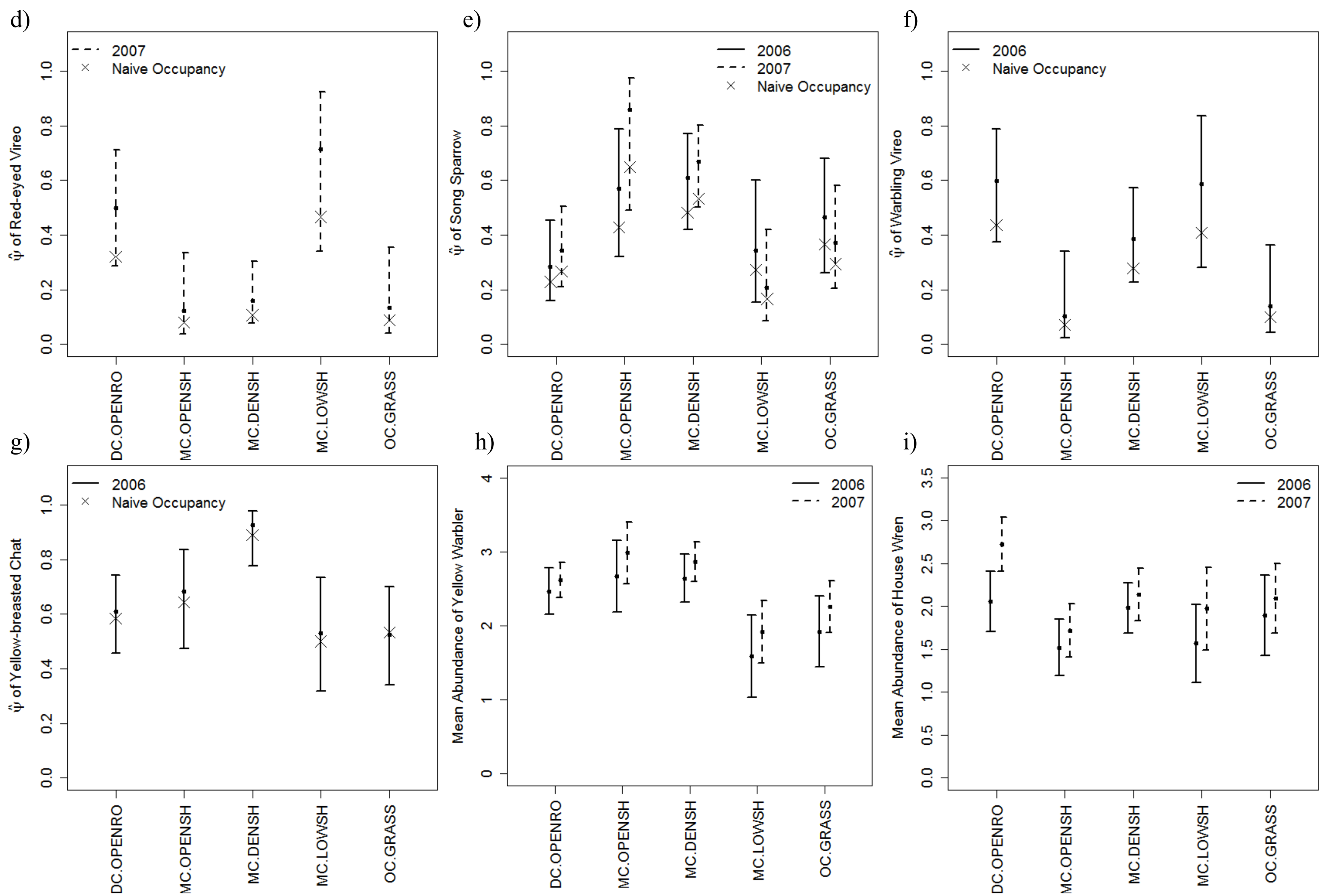


Figure 11 continued.



Least Flycatcher. Least Flycatchers were observed at 69% of cottonwood sites in at least one of the two years (Appendix 1); 61% of sites in 2006 and 64% in 2007. The single top-ranking ψ model included all predictor variables except LNSETT (Table 8). HAB received a very high cumulative model weight ($w_i = 0.99$; Table 9), suggesting that this variable had a strong influence on ψ for flycatchers. Foraging and nesting guild associations for least flycatchers predict a preference for habitats with an open understory and well-developed canopy (Table 3), and this is supported by the data. Estimated ψ was highest in the DC.OPENRO habitat (Figure 11c), where canopy cover is greatest and the understory is relatively open (Table 6). Flycatchers forage by catching insect prey on the wing, and habitats with an open understory would provide better opportunities for this foraging strategy. Additionally, the high abundance of small trees in the DC.OPENRO habitat (Table 6, Figure 3a) would provide opportunities for nesting in the lower canopy, where this species prefers to nest (Table 3). However, flycatchers were one of the most common species, and ψ was relatively high in all habitats (estimates > 0.50; Figure11c).

There was strong evidence that FCOV was positively related to ψ (Table 10, Figure 9b), which was consistent with expectations for this species (Table 3). Occupancy rate was negatively related to LNCROP (Table 10, Figure 12a), suggesting that flycatchers were more likely to occupy sites when crop fields were nearer to the riparian zone. This relationship with LNCROP was also quadratic, with high rates of predicted occupancy at intermediate values of LNCROP (Table 10, Figure 12a). Finally, RKM had a positive main and quadratic effect on ψ. Flycatchers exhibited higher ψ at sites with highest and lowest RKM, and lowest ψ at intermediate values of RKM (Table 10, Figure 10c).

Ovenbird. Ovenbirds (*Seiurus aurocapilla*) were observed at 25% of cottonwood sites in at least one of the two years (Appendix 1); 13% of sites in 2006 and 21% in 2007. FCOV, $FCOV^2$, LNSETT, and RKM were included in top-ranking ψ models (Table 8). There was strong evidence for a positive relationship between FCOV and occupancy rate (Table 10, Figure 9b), which was consistent with the expectation that forest cover would be very important for this interior habitat species (Table 3). Distance to settlement was included in one of the two top-ranking models, but evidence for a relationship between ψ and LNSETT was weak; the direction of the relationship was not consistent over the two years (i.e. negative in 2006 and positive in 2007), 95% CIs overlapped zero in all cases (Table 10), and cumulative model weight was low ($\sum w_i = 0.31$; Table 9). Consequently, there was little support for the expectation that ovenbirds would be positively associated with LNSETT (Table 3). A strong negative relationship with RKM was evident (Table 10). Estimated ψ for ovenbirds was highest at low RKM and declined in the upstream direction, suggesting that ovenbirds were more likely to occupy sites near the mouth of the river (Figure 10c). There was no evidence that LNCROP or HAB influenced ψ for ovenbirds (Table 8, Table 9). This was consistent with my expectation that habitat type would not be important for this species.

Red-eyed Vireo. Red-eyed vireos (*Vireo olivaceous*) were observed at 32% of cottonwood sites in at least one of the two years (Appendix 1); 27% of sites in 2006 and 20% in 2007. Due to problems with model convergence for the 2006 data, only data from 2007 were used in analysis. A single top-ranking model for ψ included only HAB and RKM (Table 8). HAB received a very high cumulative model weight ($\sum w_i = 0.97$; Table 9), suggesting that this variable had a strong influence on ψ relative to other variables. Estimated ψ was highest in the

DC.OPENRO and MC.LOWSH habitats, and this trend was relatively strong (Figure 11d). Vireos forage in the high canopy and nest in the lower canopy (Table 3), and DC.OPENRO would provide high levels of canopy cover for foraging and nesting opportunities (Figure 3f). Vireos share nesting and foraging guild membership with yellow warblers (Table 3), who also were found at higher abundances in the DC.OPENRO habitat type.

There was strong evidence for a negative relationship with RKM, with vireos more likely to occupy sites near the mouth of the river (Table 10, Figure 10a). Vireos were expected to exhibit a positive relationship with both FCOV and LNSETT (Table 3). However, this was not supported by the data, as neither FCOV or LNSETT were included in the top-ranking model (Table 8), and both variables received low cumulative model weights ($\sum w_i \leq 0.24$; Table 9).

Song Sparrow. Song sparrows (*Melospiza melodia*) were observed at 51% of cottonwood sites in at least one of the two years (Appendix 1); 36% of sites in 2006 and 41% in 2007. The single top-ranking model for ψ included all variables except LNCROP (Table 8). There was evidence that local habitat was influential on occupancy rates, as most higher- ranking models included HAB ($\sum w_i = 0.97$; Table 9). Estimated ψ was highest in MC.OPENSH and MC.DENSH (Figure 11e), the habitats with tall native shrub in the understory, and lowest in DC.OPENRO and MC.LOWSH, habitats with a less developed understory (Table 6). Trends were consistent across years, but differences in ψ across habitats were most evident in 2007 (Figure 11e). Song sparrows forage primarily in lower vegetation (Table 3), which would predict a preference for habitats such as MC.OPENSH and MC.DENSH that have a shrub component to the understory (Table 6).

Evidence for a negative relationship with FCOV was strong (Table 10, Figure 9a), which was consistent with expectations for this edge-habitat species (Table 3); 95% CIs for parameter estimates did not overlap zero in 2006, and the trend was marginally significant in 2007 (Table 10). Furthermore, FCOV received a high cumulative model weight ($\sum w_i = 0.99$; Table 9). The effect of LNSETT was negative and marginally significant at the 95% confidence level in one year (Table 10), which does not support the expectation that song sparrows would respond positively to distance to settlement (Table 3). Finally, the main effect of RKM on ψ was positive, suggesting that sparrows were more likely to occupy sites farther from the mouth of the river (Table 10, Figure 10b). We had expected that ψ would be negatively related to LNCROP; this was not supported by the data, as LNCROP had little influence on sparrow ψ (Table 9).

Spotted Towhee. Spotted towhees (*Pipilo maculatus*) were observed at 54% of cottonwood sites in at least one of the two years (Appendix 1); 48% of sites in 2006 and 40% in 2007. LNSETT, $LNSETT^2$, RKM and RKM^2 were included in the two top-ranking models for ψ (Table 8). HAB was not included in top-ranking models and received a low cumulative model weight ($\sum w_i = 0.19$; Table 9), suggesting habitat type did not influence towhee ψ very much. Many of the other ground-nesting species, such as common yellowthroats and ovenbirds (Table 3), also did not show a strong preference for any particular habitat types.

The main effect of LNSETT was negative, which was contrary to the expectation for towhees (Table 3). However, evidence for this relationship was weak, as 95% CIs overlapped zero in both years. A negative quadratic effect of LNSETT was marginally significant in one year (Table 10). There was evidence for a negative main effect and a negative quadratic effect of RKM on ψ (Table 10), which suggests that occupancy rate for towhees was higher near the mouth of the river and at intermediate levels of RKM, and declined at higher values of RKM

(Figure 10a). We had expected that ψ would be negatively related to distance to crop and percent forest cover (Table 3). However, FCOV and LNCROP were excluded from top-ranking models, and both received low cumulative model weights ($\sum w_i \leq 0.18$; Table 9), suggesting that these variables were not influential on ψ.

<u>Warbling Vireo</u>. Warbling vireos (*Vireo gilvus*) were observed at 38% of cottonwood sites in at least one of the two years (Appendix 1); 27% of sites in each of 2006 and 2007. Due to problems with model convergence for the 2007 data, only data from 2006 were used in analysis. Top-ranking models included all predictor variables as covariates for ψ (Table 8). HAB received the highest cumulative model weight of all variables in the top-ranking model ($\sum w_i = 0.94$; Table 9), suggesting that local habitat characteristics were relatively influential on ψ for vireos. Estimated ψ was highest in the DC.OPENRO and MC.LOWSH habitats and lowest in OC.GRASS and MC.OPENSH (Figure 11f). Both DC.OPENRO and MC.LOWSH provide relatively high levels of canopy cover (Figure 3f), which would be beneficial for warbling vireos, who forage and nest in the high canopy (Table 3). Conversely, OC.GRASS provides the lowest levels of canopy cover (Figure 3f). Habitat preferences were similar to red-eyed vireos, who also forage in the high canopy (Table 3).

There was strong evidence that FCOV and LNSETT both had a positive effect on ψ (Table 10, Figure 9b, Figure 13a), which was consistent with the expected response of vireos to these variables (Table 3). This suggests that vireos were more likely to occupy sites with higher percent forest cover and sites that were farther from human settlement. LNCROP had a negative effect (Figure 12a), but this relationship was only marginally significant at the 95% confidence level (Table 10). The positive effect of RKM was included in one of the two top-ranking models, but the evidence for this relationship was weak; the CI overlapped zero (Table 10), and the cumulative model weight was not high ($\sum w_i = 0.51$; Table 9).

<u>Western Wood-pewee</u>. Western wood-pewees were observed at 68% of cottonwood sites in at least one of the two years (Appendix 1); 62% of sites in 2006 and 53% in 2007. All variables except HAB were included in top-ranking models for ψ (Table 8). Cumulative model weight for habitat type was very low ($\sum w_i = 0.04$; Table 9), further suggesting that local habitat was not important to pewees. There was strong evidence for a positive effect of FCOV on ψ (Table 10, Figure 9b), which was contrary to the expectation that pewees would exhibit a negative response to forest cover (Table 3). The relationship between LNCROP and ψ was negative (Table 10, Figure 12a), suggesting that pewees were more likely to occupy sites that were nearest to crop fields, and providing support for the expected response of pewees to LNCROP (Table 3). However, 95% CIs overlapped zero in one of the two years (Table 10). The main effect of LNSETT was positively, but not significantly, related to ψ. There was some evidence (i.e. CIs did not overlap zero in one year; Table 10) that the relationship was quadratic, with highest ψ at intermediate values of LNSETT (Figure 13a). River location had a positive main and quadratic effect on ψ (Table 10, Figure 10b), and the evidence for this relationship was strong; RKM was included in both top-ranking models (Table 8), CIs for the main effect did not overlap zero in either year (Table 10), and cumulative model weight was high for this variable ($\sum w_i = 1.0$; Table 9).

Figure 12. Effect of log distance to crop on the occupancy or abundance of five species of birds, including a) gray catbird, least flycatcher, warbling vireo, and western wood-pewee, and b) yellow warbler. Occupancy or abundance was estimated using the highest ranking model that included log distance to crop for each species. Parameter estimates from 2007 were used unless estimates were not available for that year, then 2006 estimates were used. All other variables included in the model were held constant at their mean values, except for the categorical variable HAB, which was held constant at habitat type 'DC.OPENRO'. Points and error bars on the lines of predicted occupancy rate (ψ) represent estimated occupancy and 95% confidence intervals at the approximate 1st and 3rd quartile values for log distance to crop. Gray lines bordering the black line of predicted abundance for yellow warblers represent 95% confidence bands on those predicted values.

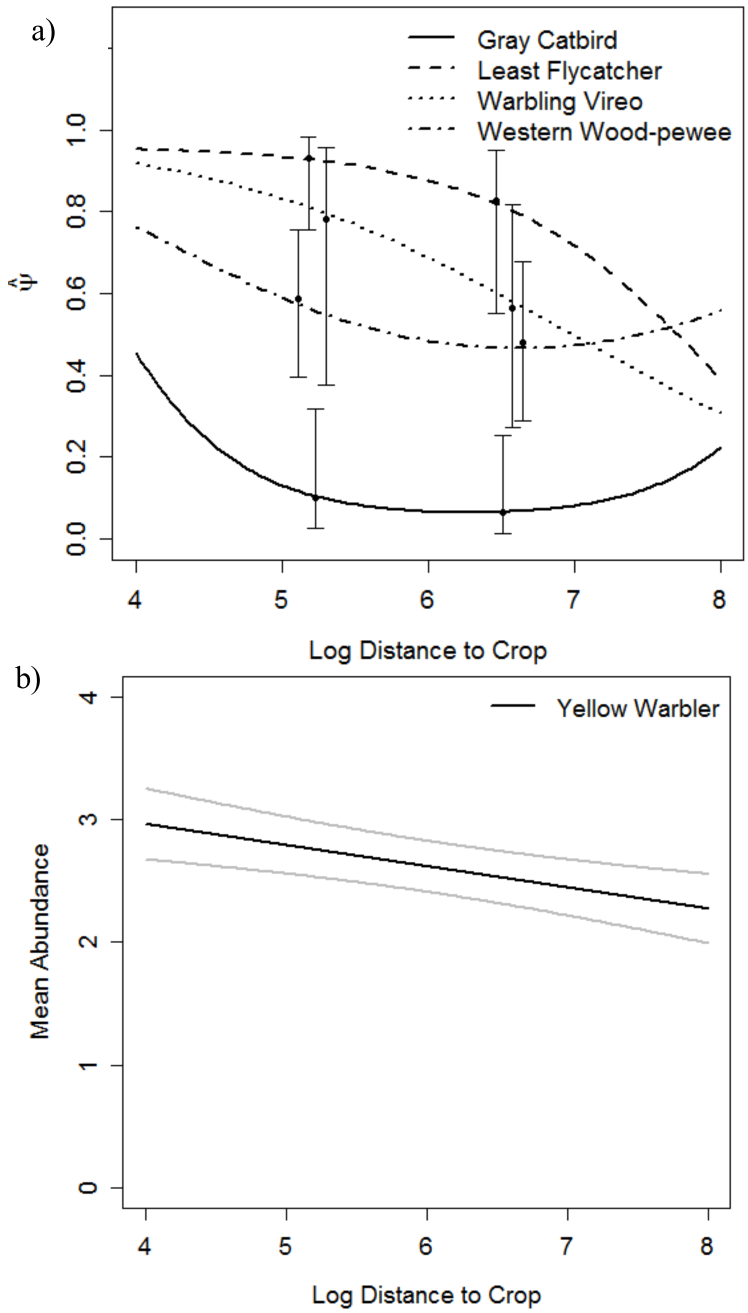
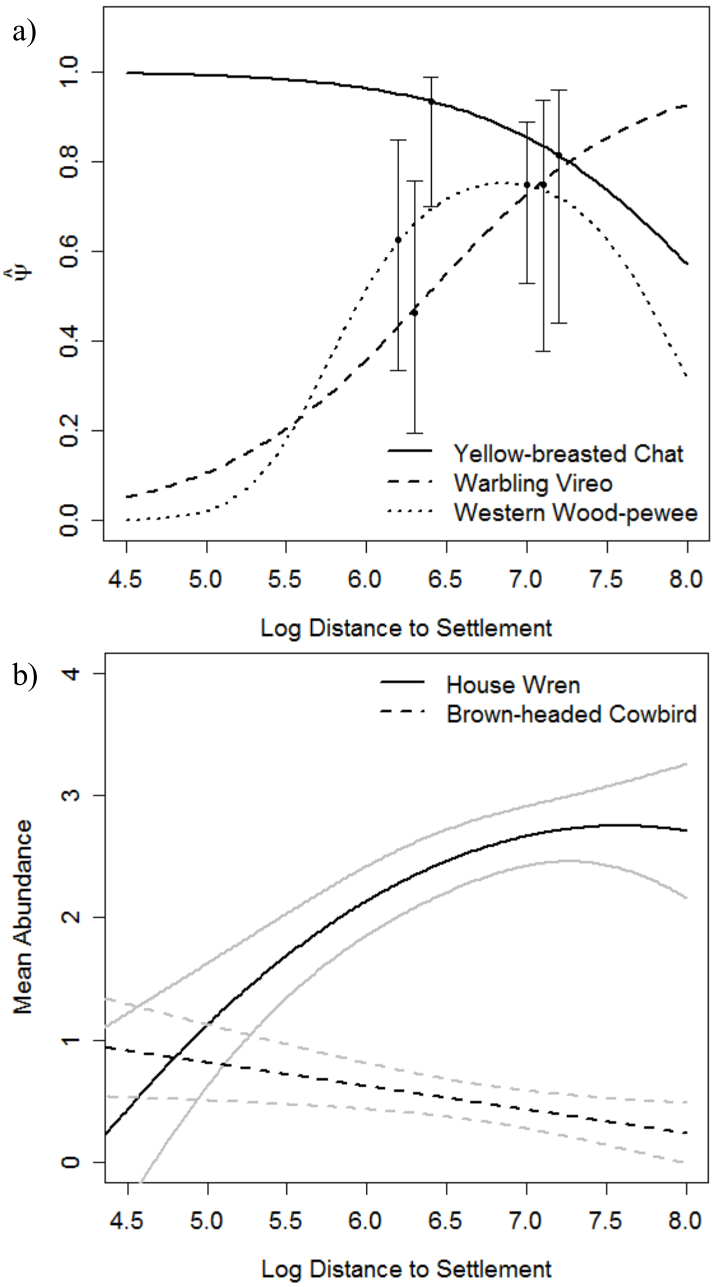


Figure 13. Effect of log distance to settlement on the occupancy or abundance of five species of birds, including a) yellow-breasted chat, warbling vireo, and western wood-pewee, and b) house wren and brown-headed cowbird. Occupancy or abundance was estimated using the highest ranking model that included log distance to settlement for each species. Parameter estimates from 2007 were used unless estimates were not available for that year, then 2006 estimates were used. All other variables included in the model were held constant at their mean values, except for the categorical variable HAB, which was held constant at habitat type 'DC.OPENRO'. Points and error bars on the lines of predicted occupancy rate (ψ) represent estimated occupancy and 95% confidence intervals at the approximate 1st and 3rd quartile values for log distance to settlement. Gray lines bordering the black lines of predicted abundance represent 95% confidence bands on those predicted values.



Yellow-breasted Chat. Yellow-breasted chats were observed at 74% of cottonwood sites in at least one of the two years (Appendix 1); 66% of sites in each of 2006 and 2007. Due to problems with model convergence for the 2007 data, only data from 2006 were used in analysis. The single top-ranking model for ψ included HAB, LNSETT, RKM, and RKM^2 (Table 8). HAB received a very high cumulative model weight compared with other variables ($\sum w_i = 0.94$; Table 9), suggesting that local habitat characteristics were relatively influential on ψ of chats. Estimated ψ was highest in the MC.DENSH habitat type (Figure 11g). Chats nest and forage in the shrub layer, so their apparent preference for a habitat type with a well-developed shrub understory is not surprising. However, ψ was relatively high in all habitats ($\psi \geq 0.4$; Figure 11g).

There was strong evidence for a negative relationship between LNSETT and ψ (Table 10, Figure 13a), suggesting that chats were less likely to occupy sites that were farthest from human settlement. This was contrary to the expectation that chats would exhibit a positive response to LNSETT (Table 3). RKM had a negative main effect on ψ, with evidence for an additional negative quadratic effect (Table 10). This suggests that occupancy rates were generally highest at intermediate values of RKM, and lowest in the western reaches of the river (Figure 10c). Forest cover and distance to crop were expected to have a negative effect on ψ (Table 3), but this was not supported by the data; FCOV and LNCROP were excluded from the top-ranking model (Table 8), and both variables had relatively low cumulative model weights ($\sum w_i \leq 0.23$; Table 9).

Yellow Warbler. Yellow warblers were observed at 99% of cottonwood sites in at least one of the two years (Appendix 1); 95% of sites in 2006 and 98% in 2007. The two top-ranking models for abundance included all predictor variables (Table 8). There was evidence that year (YR.2007) had an effect on the estimated mean abundance of birds, with higher estimates of abundance in 2007 ($\beta = 0.24$, 95% CI: 0.08,0.39). This could be due to real differences in the number of birds present over the two years, or differences in detection rates of birds resulting from observer effects. All predictor variables except LNSETT received very high cumulative model weights ($\sum w_i \geq 0.99$; Table 9). Mean abundance of yellow warblers was highest in the DC.OPENRO, MC.OPENSH, and MC.DENSH habitats (Figure 11h). Yellow warblers nest in the understory and lower canopy, and forage in the lower and higher canopy (Table 3). These three habitat types provide high percent canopy cover, as well as structural diversity in the lower canopy and understory (Table 6), which would provide abundant foraging and nesting opportunities for yellow warblers.

There was evidence for a positive effect of FCOV (Table 10, Figure 9c), which contradicted the expectation that yellow warblers would show a negative response to FCOV (Table 3). However, the relationship between LNCROP and abundance was negative (Table 10, Figure 12b), which supported expectations for this species (Table 3). Mean abundance was positively related to RKM (Table 10), suggesting that mean abundance of yellow warblers was lowest near the mouth of the river and increased steadily upstream (Figure 10d). Distance to settlement was included in one of the top-ranking models (Table 8), but the evidence for the observed negative effect of LNSETT was weak; the 95% CI substantially overlapped zero (Table 10), and the cumulative model weight for this variable was low ($\sum w_i = 0.36$; Table 9).

House Wren. House wrens were observed at 97% of cottonwood sites in at least one of the two years (Appendix 1); 92% of sites in 2006 and 94% in 2007. The single top-ranking model for mean abundance included all variables except LNCROP (Table 8). There was evidence that year had an effect on the estimated mean abundance of birds, with higher observed abundance in 2007 (β = 0.31 95% CI: 0.18,0.44). All variables present in the top-ranking model received high cumulative model weights ($\sum w_i \geq 0.95$; Table 9), suggesting that each of these variables were relatively influential on the mean abundance of house wrens. Mean abundance of wrens was constant across all habitats in both years, with the exception of habitat DC.OPENRO in 2007, when abundance was higher than in all other habitats (Figure 11i). House wrens nest in natural cavities, which are generally found in older, larger cottonwood trees. The abundance of large cottonwood trees is relatively constant across habitat types (Figure 3b), so this nesting requirement would not restrict wrens to any particular habitat type. Although wrens spend much of their time foraging in the understory, they will also forage on the ground and in the canopy (Johnson 1998), which may explain why they are found at high abundances in a variety of habitats(Figure 11i).

There was strong evidence that FCOV had a positive effect on mean abundance (Table 10, Figure 9c), which contradicted the expectation for this species (Table 3). The main effect of LNSETT on wren abundance was positive, with evidence for an additional negative quadratic relationship, suggesting that mean abundance was higher at intermediate and high values of LNSETT (Table 10, Figure 13b). RKM had a positive effect (Table 10), with mean abundance of house wrens lowest near the mouth of the river and increasing in the upstream direction (Figure 10d). LNCROP was expected to have a negative effect on house wren abundance (Table 3), but this was not supported by the data (Table 9).

Brown-headed Cowbird. Brown-headed cowbirds were observed at 74% of cottonwood sites in at least one of the two years (Appendix 1); 57% of sites in 2006 and 62% in 2007. FCOV, LNCROP, LNSETT, RKM, and RKM^2 were included in the two top-ranking models of abundance (Table 8). HAB was not included in the candidate model set for cowbirds (Table 5). Estimates of abundance were higher in 2007, although 95% CIs overlapped zero slightly (β = 0.10 95% CI: -0.04,0.24). There was strong evidence that both FCOV and LNSETT had a negative effect on cowbird abundance (Table 10, Figure 9c, Figure 13b), suggesting that cowbirds are more abundant in areas of low forest cover and areas nearer to human settlement. This was consistent with the expected responses to these variables (Table 3). The observed effect of LNCROP was also negative, but the evidence for this relationship was not strong, as 95% CIs overlapped zero (Table 10). The main and quadratic effects of RKM were both positive (Table 10), suggesting that cowbirds have higher abundance at sites in the western region, and abundance declines at intermediate and low values of RKM (Figure 10d). The cumulative model weight for RKM was higher than all other variables ($\sum w_i = 0.99$; Table 9), indicating that river location was very influential on the mean abundance of cowbirds. HOST was excluded from top-ranking models and received a cumulative model weight of only 0.07; consequently, the expectation that host abundance would positively affect cowbird abundance was not supported by the data.

Table 11. Parameter estimates representing the slope of the relationship between habitat variables and species richness or the mean abundance of five bird species. Results for all variables included in models are reported. Asterisks following estimates denote the level of significance for the slope of the relationship: * p < 0.10, ** p < 0.05, *** p < 0.01.

	Vegetation Variables						
Species or Richness	Small dbh tree	Large dbh tree	Low native shrub	Tall native shrub	Russian olive	Canopy Cover	River Kilometer
House Wren	0.031	0.458***	0.138***	-0.122***	-0.081***	0.012**	0.0020***
Least Flycatcher	0.006	0.114	0.028	-0.056**	-0.036*	0.019***	0.0007***
Western Wood-pewee	-0.020*	0.039	0.004	-0.011	-0.024**	0.007***	0.0009***
Yellow Warbler	-0.016	-0.166	-0.001	0.116***	0.033	0.015***	0.0029***
Yellow-breasted Chat	-0.010	-0.137*	0.020	0.089***	0.064***	0.002	-0.0004*
Total Richness	-0.008*	0.256	-0.072	0.233***	0.010	0.020**	0.002***
NTM Richness	-0.008	-0.053	-0.061	0.178***	0.030	0.028***	0.002***

Russian Olive and Bird Abundance or Richness

Of the five species included in analysis, four species exhibited a significant relationship between bird abundance and abundance of Russian olive. However, there was no evidence that either total species richness or NTM richness were related to Russian olive (Table 11). Six other environmental variables were also included in models; parameter estimates reflect the effect of each variable while simultaneously accounting for the influence of the other variables also included in the models. This reduces the incidence of spurious results due to correlations between Russian olive and other environmental variables. Correlations were generally low between Russian olive and the other six variables; Pearson correlation coefficients were less than 0.27 in all cases. Russian olive abundance was negatively related to mean abundance for three species, including house wrens, least flycatchers, and western wood-pewees (Table 11). Russian olive is a taller shrub, and the abundance of all three of these species was also negatively related to the abundance of tall native shrubs (Table 11). This suggests that these species may be responding negatively to structural complexity in the understory in general, and not necessarily to the presence of Russian olive. This makes sense, as least flycatchers and western wood-pewees are aerial foragers that likely need a more open understory for flycatching insects from the air (Table 3). Yellow-breasted chats were positively associated with abundance of Russian olive (Table 11). However, they were also positively associated with tall native shrubs (Table 11). Chats prefer habitats with thick understory vegetation, where they forage and nest in dense shrubs (Table 3); this suggests that they may be responding positively to dense understory vegetation in general, and not to Russian olive specifically.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Riparian zones constitute a very small portion of the landscape, yet they provide some of the most diverse and productive habitats in the western US (Kauffman et al. 2001). Cottonwood forests often provide the only extensive tracts of lowland deciduous forest, so that species dependent upon deciduous habitats are often found only in riparian forest (Palmer and Bennett 2006). Although riparian habitats are so important to sustaining diversity within the larger landscape, most riparian zones of major river systems have been severely altered by river management activities. Flows are regulated and migrating channels stabilized, resulting in the loss of successional processes driven by flood disturbance, and a decline in the rate of forest regeneration (Hupp and Osterkamp 1996). Consequently, river systems that still experience seasonal flood cycles and maintain complex geomorphic characteristics, such as multi-channeled segments and areas of extensive channel migration, are especially important for providing habitat for native wildlife communities. These river systems are also crucial for providing information about the structure and functioning of wildlife communities in relatively intact riparian ecosystems.

In this study, we had the opportunity to gather information about the riparian birds of the Yellowstone River, one of the last undammed rivers in the lower 48 states. Prior to the efforts of this study and a pilot study conducted in 2005 (Jones and Hansen 2006), few data existed about the bird species breeding in riparian habitats of the Yellowstone. This study will provide valuable information about what species are present, and how they are distributed within the floodplain. This type of basic information is essential for understanding the potential consequences of river management on bird communities. Furthermore, we have examined how factors such as local habitat characteristics, forest cover, and land use may affect the diversity, distribution, and abundance of birds. This information will provide a more comprehensive understanding of the complex relationships between birds and their environment, and allow for the formulation of management plans that take these complex relationships into account.

A diversity of habitats exist within the floodplain of the Yellowstone River. Even within a single general habitat such as mature cottonwood forest in multi-channel reaches, a variety of types were identified. Cottonwood forest habitat types differed in structural characteristics of the understory and canopy, including shrub density and height, size and density of trees, and percent canopy cover. The density of exotic Russian olive also differed across particular habitat types (Table 6). Differences in characteristics of cottonwood forest may represent underlying local gradients in forest age, time since last disturbance, or variation in geomorphic conditions. Therefore, the diversity of cottonwood habitats observed within the floodplain may exist because of the interaction between natural geomorphic heterogeneity within the floodplain and the impacts of regular flood disturbance. Both of these processes are altered when management activities, such as channel stabilization or the construction of dams, result in the reduction of channel migration, loss of side channels, or significant channel dewatering.

Four of the five cottonwood habitats were distributed relatively evenly along the length of the study area (Figure 4). This suggests that flood disturbance and geomorphic heterogeneity also occur along the length of study area. Geomorphic classification of the river confirms this, as the four types of reaches that were sampled are relatively well-represented from one end of the study area to the other (Appendix 2). It is important to remember that only braided and anabranching reaches were sampled for this study; a random sample of reaches within the entire study area would likely exhibit broad scale patterns across sections of the river due to differences in underlying geomorphology or impacts of flood disturbance. However, an investigation that focuses only on multi-channel reaches is highly relevant for understanding the importance of riparian habitats to birds, as these areas harbor the most extensive and heterogeneous riparian zones and the highest bird diversity. Finally, the sites surveyed were not from a purely random sample, as only areas accessible by foot were included. Patterns in the distribution of habitats along the river may emerge if islands and isolated gravel and sand bars were included in the sample. Therefore, inference about the distribution of habitats is limited to mature cottonwood forests that are connected to the mainland.

Local habitat characteristics were important drivers of bird distribution and abundance. Most species exhibited a positive or negative association with at least one cottonwood habitat type, when compared with other cottonwood habitats that were sampled. This was apparent for very abundant species, such as yellow warblers (Figure 11h) as well as less common species, such as red-eyed vireos (Figure 11d). Habitat preferences tended to reflect the niche requirements of each species. A variety of species were observed breeding within cottonwood forest habitats, ranging from species that nest and forage in the canopy (e.g. warbling vireos), to those that nest and forage on the ground (e.g. ovenbirds; Table 3). This suggests that the existence of a variety of cottonwood habitat types within the floodplain is a major factor contributing to the diversity of bird communities within the riparian zone. This is further supported by results from the guild richness analyses. Certain cottonwood habitats supported higher numbers of species that used particular resources than did other cottonwood habitats, suggesting that different habitats provide different types of resources for birds. For example, richness of species that forage on the ground was highest in the habitats with the greatest densities of native shrub (Table 7). Furthermore, the habitat with the highest canopy cover (DC.OPENRO) supported the greatest number of species that forage in the canopy. This habitat also supported the fewest number of species that nest and forage on the ground (Table 7). Structural complexity within cottonwood forest habitats also seemed to be an important factor, as the habitats with the most complexity in the understory and canopy also reported the highest total and NTM species richness (Figure 6).

Management activities that reduce the extent, heterogeneity, and complexity of cottonwood habitats within the floodplain will likely result in the loss of certain riparian bird species and a decline in bird species richness. For example, if the extent of younger cottonwood habitats are reduced as a result of declines in cottonwood regeneration, bird diversity would probably also decline because the cottonwood habitats that likely represent older cottonwood forests (MC.LOWSH and OC.GRASS) have lower overall species richness (Figure 6), and support few species that nest and forage in the understory (Table 7).

Patterns in the amount of forest cover within cottonwood forests were not apparent along the length of the river, suggesting that a variety of forest cover conditions were available within all multi-channel sections that were sampled. The amount and density of forest cover is an important habitat characteristic for bird species in general (McGarigal and McComb 1995, Trzcinski et al. 1999). There was strong evidence that it was very important to the riparian birds breeding along the Yellowstone River as well. Responses of bird species to forest cover were predictable based on life history traits of each species (Table 3). Species that prefer interior forest conditions generally had a positive association with forest cover, while edge species often exhibited a negative response. Edge species generally prefer habitats with a lower forest cover because these habitats also have a dense understory of shrubs for foraging and nesting (Table 6). However, three 'edge' species responded positively to forest cover (Table 10). These species also were positively associated with crop fields, suggesting that some edge species may prefer dense forest cover, as long as there are other edge habitats (such as those created by adjacent fields) nearby.

Cottonwood forests are patchy in nature due to the frequent impacts of flood disturbance. However, forests along the Yellowstone River supported not only species that prefer patchy habitats, but also species that are associated with more contiguous forest habitats (Table 3). This suggests that the existence of a variety of forest cover conditions within the floodplain is important for maintaining populations of riparian breeding bird species, and overall bird diversity. This may be particularly true for species that are dependent upon interior forests (e.g. ovenbirds; Table 3), because these types of forest conditions are relatively limited within the naturally patchy habitats of the floodplain. Management activities that result in the transition of habitats to older, more open forests, and reduce the area of forest cover in the floodplain may be especially detrimental to those species that are dependent upon habitats with dense forest cover.

The percent forest cover surrounding a survey site is an accurate measure of the density of forest cover within the area inhabited by breeding birds at a site. This has been demonstrated to be an important measure of habitat condition for birds, and was important in our examination of riparian birds along the Yellowstone River. However, percent forest cover does not necessarily represent the overall width of the riparian zone, which has also been identified as an important driver of bird distribution as well (Hodges and Krementz 1996, Hagar 1999). Floodplain width generally increases downstream, and the width and total area of cottonwood forests likely also increases. Trends in bird responses to forest cover at this broader scale would likely reflect those that we found at the scale of the survey site, with forest interior species positively associated with wider tracts of riparian forest. Wide and extensive cottonwood forests are associated with frequent flood disturbance and the migration of the river channel within this wider floodplain (Hupp and Osterkamp 1996). This again suggests that the existence of natural geomorphic conditions (such as the downstream increase in floodplain area) and the impacts of regular flood disturbance are crucial for the maintenance of bird populations and bird diversity at the scale of the entire river system.

Land use can have a substantial impact on characteristics of bird communities. Consequences of land use are usually manifest through declines in nest productivity or increases in adult mortality due to changes in predator and parasite communities (Bayne and Hobson 1997, Tewksbury et al. 1998, Marzluff et al. 1998, Rodewald and Shustack 2007, Vander Haegen 2007). Therefore, it may be difficult to observe the impacts of land use on bird communities solely using presence/absence data (i.e. such as the data collected during point count surveys). However, many species in this study exhibited significant responses to the proximity of agriculture and human settlement. Four species (least flycatcher, warbling vireo, western wood-pewee, and yellow warbler) had higher occupancy or abundance at sites where crop fields were close to the riparian zone (Figure 12). Most of these species prefer habitats with high canopy cover, but also use edge habitats (Table 3). Crop fields may provide an abrupt edge that is otherwise not common in cottonwood forests with higher canopy cover. This suggests that agriculture adjacent to the riparian zone may affect bird communities by influencing the availability of certain habitat types, not just by impacting survival or productivity. This may be particularly relevant in riparian ecosystems, where the total area of habitat is small and agriculture is very close to the riparian zone. If the area of forest within the floodplain is reduced as a result of the addition of crop fields, then species that depend on more extensive tracts of forest could be negatively impacted by the presence of agriculture. However, significant negative associations with crop fields were not evident for any of the species in our analysis.

Human settlement was highest in the western region of the study area near the foothills of the mountains, and declined linearly toward the mouth of the river (Figure 5c). This suggests that a variety of conditions in land use existed along the length of the study area. Birds seemed to respond to the distribution of human settlement within the floodplain, as five species exhibited a significant relationship with this variable (Figure 13). Brown-headed cowbirds were one of the two species for which the association was positive. We expected cowbirds to show an affinity for areas that were closer to human settlement, because they forage in areas with higher densities of livestock (such as feedlots or farmsteads). Cowbirds lay their eggs in the nests of other songbird species (Table 3), and have been shown to have a negative effect on many species of riparian birds by reducing productivity below levels needed to sustain populations. Because of this, we expected that species that are cowbird hosts would respond negatively to the presence of human settlement. Warbling vireos are a very common cowbird host, and did show a significant negative association with settlement (i.e. a positive association with distance to settlement; Figure 13a). Other studies have documented the detrimental effect of cowbirds on warbling vireos nesting in cottonwood habitats (Tewksbury et al. 1998, 2006); therefore, the apparent avoidance of cottonwood forest near human settlement on the Yellowstone River may also reflect the influence of cowbirds on vireo productivity.

It is well-documented that human land use in close proximity to riparian habitats can substantially influence bird communities in general (Hennings and Edge 2003, Miller et al. 2003, Rottenborn 1999, Lussier et al. 2006), and we have presented evidence that land use does influence some of the riparian bird species breeding along the Yellowstone River. This has direct implications when considering the influence of management activities that result in the expansion of particular land uses within or adjacent to the riparian zone. However, there are also implications for the indirect management effects of land use on bird communities. Increased agricultural production or human settlement within the floodplain may increase the need for bank stabilization or water management to reduce the loss of land and property from natural flooding or erosion. Furthermore, if river management activities result in a reduction in the extent and quality of habitats available to birds, the additional negative influences of land use on bird productivity may compound the stresses on bird populations so that consequences of management are more severe than anticipated. Therefore, it is important to understand how birds may be influenced by surrounding land use, and consider these potential effects when formulating plans for management within the river channel and floodplain.

Even after accounting for the effects of local habitat, forest cover, and land use, river location was one of the most important factors influencing the abundance and distribution of bird species. All but one of the 14 focal species exhibited a significant relationship with river location. Additionally, many of the other riparian species observed were differentially distributed amongst reaches of the river (Appendix 3). Most of the relationships with river location were either negative or positive (i.e. higher abundance or occupancy at one end of the study area or the other), with only a couple of species exhibiting low or high abundance or occupancy in the middle reaches of the river (Figure 10). Bird species richness was also dependent upon river location. At cottonwood forest sites, richness was higher in the western region of the study area and lowest within intermediate reaches (Figure 7a). This pattern was also evident within cottonwood habitat types (Figure 7c, 7d), suggesting that the effect was due to river location, and not changes in habitat characteristics along the river.

The influence of river location may reflect the distribution of resources important to birds that change from the headwaters to the mouth of a river. For example, it has been documented that the abundance and diversity of insects change predictably along the length of a river (Vannote et al. 1980, Reese and Batzer 2007, Arscott et al. 2005, Growns and Davis 1994, Vinson and Hawkins 1998). We were not able to examine relationships between bird abundance or distribution and food resources, yet the availability of food is a crucial component of habitat quality. Birds may specialize on a particular type of food, so that different bird species would respond differently to gradients in food resources. Other underlying gradients may exist that we were not able to measure, such as changes in climate that would influence habitat condition in subtle ways (e.g. variation in the time that vegetation first produces leaves in the spring, differences in humidity that influence microclimates within forests, etc.). By examining the influences of river location, we may be quantifying the influences of these types of unmeasured gradients on the distribution and abundance of birds.

Bird response to changing river location may also reflect broader scale influences on bird distribution, such as the geographic range of a species within a region or continent. The density of a species is usually highest at the core of its range, and declines as distance from the core increases (Brown 1984). Therefore, if a species breeding along the Yellowstone River is at the edge of its range, then its abundance or occupancy rate may vary by river location because of this. The study area falls within the edge of the geographic range for five of the fourteen focal species; western wood-pewees and spotted towhees range largely in the western US, while gray catbirds, red-eyed vireos, and ovenbirds range largely in the east. For three of these species, effects of river location are consistent with what would be expected based on geographic distribution. For example, red-eyed vireos exhibit a negative relationship with river kilometer (Figure 10a), indicating that they are more likely to occupy sites in the eastern end of the study area. However, for two of the species the effect of river location is opposite what would be expected based on their geographic ranges. Furthermore, many of the species have a continental distribution, but these species still exhibit strong relationships with river location. This suggests that the apparent effect of river location on bird species distribution and abundance is likely due to a combination of the influences of unmeasured environmental resources, and broad-scale geographic range distributions.

The influence of river location on riparian birds presents a challenge when considering the effects of management over a large area, such as the length of a major river system. Characteristics of local habitat, forest cover, and land use, which are some of the most important factors influencing the distribution of birds, and which are often used to measure habitat quality or suitability for a species or community, may not adequately account for the observed variation in characteristics of bird communities. Along the Yellowstone River, river location was one of the most important influences for most species. Consequently, areas with similar habitat suitability ratings may harbor different bird communities because of their location along the river. Therefore, it may be necessary to consider relationships with geographical location when attempting to understand the potential consequences of management for bird species and communities. For example, management activities may need to be considered within the context of particular reaches or ecoregions of the river, as different bird communities may be present within a given habitat type that exists in reaches or ecoregions along the length of the river.

The influence of the exotic shrub Russian olive on bird species richness was investigated, as well as its influence on the abundance of five common species. There was no evidence that species richness was affected by the abundance of Russian olive (Table 11). For four of the species included in abundance analysis, significant relationships between Russian olive abundance and bird abundance were evident (Table 11). However, for all of these species, the effect of Russian olive was similar to the effect of tall shrubs, suggesting that birds may be responding to habitat structure in general and not Russian olive in particular. These results may indicate that Russian olive alters habitat structure, and birds respond to those habitat changes. However, the relevance of this information to the management of Russian olive may be limited, as tall native shrubs have the same effect on habitat structure, and cottonwood habitats with a shrub understory are some of the most common habitat types along the river (Table 6).

It is difficult to understand how the invasion of Russian olive influences bird communities using only presence/absence bird data collected at randomly located sites. Only one study that we know of has been conducted that examines bird communities in Russian olive stands compared to native willow forest with similar structural characteristics (Brown 1990). This study along the Snake River in Idaho reported that bird species richness and abundance are higher in native forest, likely due to higher insect abundances found there. There is some evidence that Russian olive may compete with native green ash in the understory of cottonwood forests along the lower Yellowstone River of southeastern Montana (Lessica and Miles 2001). If Russian olive is excluding native shrub species in the understory of cottonwood forests, then bird species richness and abundance may decline due to the further expansion of Russian olive trees into the riparian zone. This may be especially relevant to bird communities along the Yellowstone because highest bird species richness was observed in cottonwood forest habitats with native shrub in the understory (Figure 6). Russian olive is a later-seral species compared to most native riparian plants. Therefore, management activities that regulate flows and limit flood disturbance may allow for the persistence of higher elevation terraces, and facilitate the expansion of Russian olive within the floodplain (Katz and Shafroth 2003).

Further studies that are specifically designed to investigate the influence of Russian olive are necessary to understand the real implications of its expansion into the riparian zone along the Yellowstone. First, studies would need to quantify how Russian olive is impacting native plant communities that constitute important bird habitats (e.g. is there a particular native habitat type that is being displaced by Russian olive?). Second, studies examining how birds use (or do not use) Russian olive relative to native shrubs, and how Russian olive influences measures of productivity relative to native shrub habitats would need to be implemented to understand the effect of Russian olive on habitat suitability and population demographics.

Few studies exist that document characteristics of bird communities along the length of a major river system, because it is difficult to systematically survey birds over large geographic areas, and it is often logistically complicated to gain access to private lands within riparian zones. Consequently, the information gathered in this study will provide valuable insight about the distribution of birds not only along the Yellowstone River, but also within the floodplains of major river systems in general. Few data exist that document the historical distribution of bird species within the riparian zone of the Yellowstone, so it is impossible to quantify the status of bird communities today relative to the past. However, the Yellowstone River is one of the few rivers in the western US that still experiences seasonal flooding and regular disturbance within the floodplain, which contribute to the existence of extensive native riparian plant communities. We have demonstrated that the riparian corridor provides breeding habitats and resources for many different types of bird species. Only one exotic species (the European starling) was encountered, and none of the species that we recorded are listed as federally endangered or threatened under the Endangered Species Act. This suggests that the riparian habitats along the Yellowstone River support relatively healthy populations of bird communities today. However, the brown-headed cowbird, a nest parasite that has been implicated in the decline of many North American songbird species, was one of the most abundant and widespread species that we encountered (Appendix 1). Although the historical distribution and abundance of cowbirds in the riparian zone is unknown, cowbirds are known to be positively associated with human settlement. Given that human presence in the floodplain has increased since Europeans settled the region, riparian bird populations may today be more heavily impacted by cowbird parasitism than they were historically. The knowledge acquired in this study will provide a more comprehensive understanding of the potential influences of floodplain management on riparian species, and allow for an assessment of the consequences of management for all wildlife that are dependent upon the unique habitats and resources provided by the Yellowstone River.

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APPENDIX 1. RIPARIAN BIRD SPECIES OBSERVED DURING POINT COUNT SURVEYS ALONG THE YELLOWSTONE RIVER

Appendix 1. Riparian breeding bird species detected during point count surveys at riparian sites along the Yellowstone River. Non-target species (ducks, raptors, upland gamebirds, and shorebirds) are excluded. The total number of sites that were occupied by a species in at least one of the two years is reported for cottonwood (CWFOREST), grassland (GRASS), and shrubland (SHRUB) habitats. Migratory guild denotes whether a species winters in the US and is a short-distance migrant or resident (SDR), or winters south of the US and is a Neotropical migrant (NTM). Foraging guilds denote where a species typically forages: On the ground (FGND), on the ground or in low shrubs (FLOW), in high shrubs or in the canopy layer(FCAN), on the wing (FAIR), or on the trunks and branches of trees (FTRE). Nesting guilds denote where in the understory or canopy layer a species typically places its nest: On or close to the ground (NGND), in cavities (NCAV), in shrubs or in the low canopy layer (NLOW), or in the midstory or high canopy layer (NMSC). Species not included in guild analyses were not assigned guild membership, and cells for these species are empty.

Common Name	Scientific Name	Number (%) of Sites Occupied			Guild Membership		
		CWFOREST	GRASS	SHRUB	Migratory	Foraging	Nesting
American Crow	*Corvus brachyrhynchos*	25 (11)	1 (3)	1 (3)	SDR	FGND	NMSC
American Goldfinch	*Carduelis tristis*	135 (58)	3 (10)	20 (50)	SDR	FLOW	NLOW
American Redstart	*Setophaga ruticilla*	84 (36)	1 (3)	8 (20)	NTM	FCAN	NLOW
American Robin	*Turdus migratorius*	169 (72)	7 (23)	15 (38)	SDR	FLOW	NLOW
Baltimore Oriole	*Icterus galbula*	27 (12)	0	4 (10)	NTM	FCAN	NMSC
Barn Swallow	*Hirundo rustica*	0	5 (17)	1 (3)	NTM		
Black-and-white Warbler	*Mniotilta varia*	27 (12)	0	1 (3)	NTM	FTRE	NGND
Black-billed Cuckoo	*Coccyzus erythropthalmus*	3 (1)	0	0	NTM		
Black-billed Magpie	*Pica hudsonia*	34 (15)	2 (7)	2 (5)	SDR	FLOW	NLOW
Black-capped Chickadee	*Poecile atricapillus*	98 (42)	0	7 (18)	SDR	FCAN	NCAV
Black-headed Grosbeak	*Pheucticus melanocephalus*	127 (54)	1 (3)	7 (18)	NTM	FCAN	NLOW
Blue Jay	*Cyanocitta cristata*	9 (4)	0	1 (3)	SDR		
Bobolink	*Dolichonyx oryzivorus*	4 (2)	3 (10)	3 (8)	NTM		
Brewers Blackbird	*Euphagus cyanocephalus*	10 (5)	1 (3)	5 (13)	SDR	FGND	NLOW
Brown Thrasher	*Toxostoma rufum*	20 (9)	1 (3)	6 (15)	SDR	FGND	NLOW
Brown-headed Cowbird	*Molothrus ater*	174 (74)	10 (33)	23 (58)	SDR	FGND	--
Bullock's Oriole	*Icterus bullockii*	60 (26)	3 (10)	3 (8)	NTM	FCAN	NMSC
Cedar Waxwing	*Bombycilla cedrorum*	73 (31)	0	7 (18)	SDR	FCAN	NLOW
Chimney Swift	*Chaetura pelagica*	12 (5)	6 (20)	5 (13)	NTM	FAIR	NCAV
Chipping Sparrow	*Spizella passerina*	4 (2)	0	1 (3)	SDR		
Clay-colored sparrow	*Spizella pallida*	26 (11)	1 (3)	10 (25)	SDR	FGND	NLOW
Cliff Swallow	*Petrochelidon pyrrhonota*	1 (1)	4 (13)	1 (3)	NTM		
Common Grackle	*Quiscalus quiscula*	59 (25)	3 (10)	10 (25)	SDR	FGND	NMSC
Common Yellowthroat	*Geothlypis trichas*	135 (58)	14 (47)	21 (53)	NTM	FLOW	NGND
Dickcissel	*Spiza americana*	6 (3)	2 (7)	1 (3)	NTM		
Downy Woodpecker	*Picoides pubescens*	88 (38)	0	5 (13)	SDR	FTRE	NCAV
Eastern Kingbird	*Tyrannus tyrannus*	82 (35)	11 (37)	18 (45)	NTM	FAIR	NMSC

Appendix 1 continued.

Common Name	Scientific Name	Number (%) of Sites Occupied			Guild Membership		
		CWFOREST	GRASS	SHRUB	Migratory	Foraging	Nesting
European Starling	*Sturnus vulgaris*	124 (53)	9 (30)	15 (38)	SDR	FGND	NCAV
Field Sparrow	*Spizella pusilla*	48 (21)	5 (17)	16 (40)	SDR	FLOW	NGND
Grasshopper Sparrow	*Ammodramus savannarum*	10 (5)	3 (10)	5 (13)	SDR	FGND	NGND
Gray Catbird	*Dumetella carolinensis*	129 (55)	5 (17)	14 (35)	NTM	FLOW	NLOW
Hairy Woodpecker	*Picoides villosus*	65 (28)	0	5 (13)	SDR	FTRE	NCAV
House Wren	*Troglodytes aedon*	226 (97)	8 (27)	27 (68)	NTM	FLOW	NCAV
Lark Sparrow	*Chondestes grammacus*	10 (5)	4 (13)	8 (20)	SDR	FGND	NGND
Lazuli Bunting	*Passerina amoena*	102 (44)	1 (3)	17 (43)	NTM	FLOW	NLOW
Least Flycatcher	*Empidonax minimus*	162 (69)	0	13 (33)	NTM	FAIR	NLOW
Mountain Bluebird	*Sialia currucoides*	1 (1)	0	1 (3)	NTM		
Mourning Dove	*Zenaida macroura*	131 (56)	2 (7)	12 (30)	SDR	FGND	NMSC
Northern Flicker	*Colaptes auratus*	183 (78)	1 (3)	20 (50)	SDR	FGND	NCAV
Orchard Oriole	*Icterus spurius*	3 (1)	0	1 (3)	NTM		
Ovenbird	*Seiurus aurocapilla*	58 (25)	0	7 (18)	NTM	FGND	NGND
Plumbeous Vireo	*Vireo plumbeous*	24 (10)	0	1 (3)	NTM	FCAN	NLOW
Red-eyed Vireo	*Vireo olivaceous*	76 (33)	0	2 (5)	NTM	FCAN	NLOW
Red-headed Woodpecker	*Melanerpes erythrocephalus*	24 (10)	1 (3)	4 (10)	SDR	FTRE	NCAV
Red-naped Sapsucker	*Sphyrapicus nuchalis*	2 (1)	0	0	SDR		
Red-winged Blackbird	*Agelaius phoeniceus*	51 (22)	19 (63)	16 (40)	SDR	FGND	NLOW
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	2 (1)	0	0	NTM		
Savannah Sparrow	*Passerculus sandwichensis*	10 (5)	12 (40)	8 (20)	NTM	FGND	NGND
Song Sparrow	*Melospiza melodia*	120 (51)	15 (50)	17 (43)	SDR	FLOW	NGND
Spotted Towhee	*Pipilo maculatus*	127 (54)	0	14 (35)	SDR	FLOW	NGND
Swainson's Thrush	*Catharus ustulatus*	6 (3)	0	0	NTM		
Tree Swallow	*Tachycineta bicolor*	72 (31)	11 (37)	11 (28)	NTM	FAIR	NCAV
Vesper Sparrow	*Pooecetes gramineus*	4 (2)	1 (3)	1 (3)	SDR		
Violet-green Swallow	*Tachycineta thalassina*	11 (5)	11 (37)	1 (3)	NTM	FAIR	NCAV
Warbling Vireo	*Vireo gilvus*	88 (38)	1 (3)	5 (13)	NTM	FCAN	NMSC
Western Kingbird	*Tyrannus verticalis*	10 (5)	2 (7)	5 (13)	NTM	FAIR	NMSC
Western Meadowlark	*Sturnella neglecta*	30 (13)	14 (47)	26 (65)	SDR	FGND	NGND
Western Wood-pewee	*Contopus sordidulous*	158 (68)	3 (10)	11 (28)	NTM	FAIR	NMSC
White-breasted Nuthatch	*Sitta carolinensis*	22 (9)	0	1 (3)	SDR	FTRE	NCAV
White-throated Swift	*Aeronautes saxatalis*	3 (1)	1 (3)	0	NTM		
Yellow Warbler	*Dendroica petechia*	233 (100)	13 (43)	30 (75)	NTM	FCAN	NLOW
Yellow-bellied Sapsucker	*Sphyrapicus varius*	1 (1)	0	0	SDR		
Yellow-breasted Chat	*Icteria virens*	172 (74)	4 (13)	20 (50)	NTM	FLOW	NLOW
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	1 (1)	1 (3)	0	NTM		

APPENDIX 2. DISTRIBUTION OF RIPARIAN HABITATS AND BIRD COMMUNITY CHARACTERISTICS WITHIN GEOMORPHIC REACHES ALONG THE YELLOWSTONE RIVER

Appendix 2. Distribution of riparian habitats and breeding bird community characteristics within geomorphic reaches of the Yellowstone River in 2006 and 2007. Reach type categories include: partially-confined braided (PCB), partially-confined anabranching (PCA), unconfined anabranching (UA), and unconfined braided (UB). River kilometers (km) are measured along an approximation of the centerline of the main channel, with kilometer 0 located at the mouth of the river and increasing in the upstream direction. The total number of survey sites within each reach is reported, as well as the number of sites by habitat type. Habitats include cottonwood forest (CWFOREST), grassland (GRASS), shrubland (SHRUB), and five cottonwood habitat types (DC.OPENRO, MC.OPENSH, MC.DENSH, MC.LOWSH, AND OC.GRASS). Mean bird species richness (the average number of species recorded across sites in a reach) is reported for each reach within each habitat type. Mean richness is followed in parentheses by the total number of species observed within a reach and habitat type. Mean richness is not reported for 'Total' because it would not be meaningful to calculate this value across habitat types. Summaries include 64 bird species; non-target species (ducks, raptors, upland gamebirds, and shorebirds), are excluded.

Reach ID	Reach Type	US* River Km (River mi)	DS* River Km (River mi)	Number of Sites								
				Total	GRASS	SHRUB	CWFOREST	DC. OPENRO	MC. OPENSH	MC. DENSH	MC. LOWSH	OC. GRASS
A7	PCB	727 (452)	712 (442)	27	7	3	17	4	8	1	0	4
A11	PCB	691 (429)	679 (422)	18	4	2	12	2	3	5	0	2
A12	PCB	679 (422)	670 (416)	2	0	0	2	2	0	0	0	0
A14	PCA	665 (413)	654 (406)	11	1	0	10	3	0	2	0	5
A16	PCA	643 (400)	628 (390)	12	0	0	12	0	4	7	0	1
A17	UA	628 (390)	621 (386)	7	1	0	6	1	2	2	0	1
A18	UA	621 (386)	616 (383)	7	2	1	4	2	1	0	1	0
B1	UB	616 (383)	591 (367)	17	1	1	15	1	2	9	0	3
B2	PCB	591 (367)	580 (360)	8	0	1	7	5	0	0	1	1
B3	UB	580 (360)	575 (357)	8	2	0	6	5	0	1	0	0
B5	UA	568 (353)	555 (345)	7	0	1	6	5	0	0	0	1
B6	PCB	555 (345)	547 (340)	3	0	0	3	0	0	2	0	1
B7	UB	547 (340)	532 (331)	4	0	0	4	0	2	2	0	0
B8	PCA	532 (331)	518 (322)	13	2	2	9	1	0	7	1	0
C3	UA	462 (287)	451 (280)	12	1	2	9	4	0	4	0	1
C7	UA	431 (268)	417 (259)	30	5	5	20	1	2	6	5	6
C9	UA	407 (253)	389 (242)	28	2	6	20	3	5	5	3	4
D5	PCA	170 (106)	152 (95)	9	1	2	6	2	0	2	2	0
D10	PCA	108 (67)	91 (56)	16	0	5	11	1	1	6	2	1
D11	PCA	91 (56)	81 (50)	41	1	6	34	4	7	10	9	4
D12	PCA	81 (50)	56 (35)	24	0	3	21	10	0	4	6	1

*US = Upstream, DS = Downstream

Appendix 2 continued.

Reach ID	Reach Type	US* River Km (River mi)	DS* River Km (River mi)	Mean Bird Species Richness (Total Number of Bird Species Observed)								
				Total	GRASS	SHRUB	CWFOREST	DC. OPENRO	MC. OPENSH	MC. DENSH	MC. LOWSH	OC. GRASS
A7	PCB	727 (452)	712 (442)	(43)	3.2 (24)	6.7 (31)	10.0 (34)	9.3 (26)	11.2 (32)	13.0 (17)	--	7.7 (24)
A11	PCB	691 (429)	679 (422)	(46)	2.4 (17)	7.0 (27)	9.4 (41)	8.3 (28)	9.4 (32)	9.5 (34)	--	10.2 (27)
A12	PCB	679 (422)	670 (416)	(24)	--	--	7.8 (24)	7.8 (24)	--	--	--	--
A14	PCA	665 (413)	654 (406)	(37)	4.0 (6)	--	8.0 (36)	7.0 (27)	--	9.9 (20)	--	7.8 (27)
A16	PCA	643 (400)	628 (390)	(35)	--	--	8.6 (35)	--	9.0 (29)	8.3 (29)	--	8.4 (19)
A17	UA	628 (390)	621 (386)	(37)	4.1 (15)	--	7.8 (34)	6.0 (20)	8.3 (23)	7.7 (25)	--	8.5 (19)
A18	UA	621 (386)	616 (383)	(27)	0.5 (2)	3.0 (7)	7.3 (25)	7.0 (20)	8.0 (16)	--	7.0 (10)	--
B1	UB	616 (383)	591 (367)	(42)	3.7 (7)	5.0 (8)	7.9 (41)	6.8 (17)	7.5 (18)	8.4 (37)	--	6.9 (31)
B2	PCB	591 (367)	580 (360)	(32)	--	6.8 (19)	7.0 (32)	7.3 (29)	--	--	5.7 (13)	7.3 (16)
B3	UB	580 (360)	575 (357)	(39)	3.8 (13)	--	7.6 (35)	7.8 (33)	--	7.0 (14)	--	--
B5	UA	568 (353)	555 (345)	(33)	--	8.5 (22)	8.5 (31)	8.9 (29)	--	--	--	6.8 (14)
B6	PCB	555 (345)	547 (340)	(23)	--	--	8.4 (23)	--	--	8.7 (19)	--	8.0 (15)
B7	UB	547 (340)	532 (331)	(33)	--	--	8.8 (33)	--	9.1 (29)	8.6 (24)	--	--
B8	PCA	532 (331)	518 (322)	(40)	2.7 (12)	3.0 (12)	7.9 (34)	6.3 (14)	--	8.4 (34)	6.7 (12)	--
C3	UA	462 (287)	451 (280)	(39)	2.0 (4)	7.2 (24)	7.2 (37)	7.6 (26)	--	8.6 (33)	--	8.6 (20)
C7	UA	431 (268)	417 (259)	(50)	3.3 (21)	4.7 (25)	6.9 (46)	7.6 (16)	8.1 (28)	7.3 (33)	7.1 (35)	5.9 (35)
C9	UA	407 (253)	389 (242)	(52)	5.5 (22)	6.2 (36)	7.4 (47)	8.0 (26)	8.0 (31)	7.9 (29)	6.5 (29)	6.4 (32)
D5	PCA	170 (106)	152 (95)	(33)	2.0 (3)	4.3 (11)	7.5 (30)	9.0 (20)	--	7.0 (16)	6.5 (17)	--
D10	PCA	108 (67)	91 (56)	(43)	--	4.7 (28)	8.9 (39)	7.5 (13)	10.3 (19)	9.2 (35)	9.0 (22)	6.8 (14)
D11	PCA	91 (56)	81 (50)	(51)	3.5 (6)	4.9 (36)	7.1 (50)	7.2 (30)	7.2 (40)	8.5 (45)	6.0 (39)	5.5 (26)
D12	PCA	81 (50)	56 (35)	(51)	--	5.1 (27)	9.0 (49)	8.6 (40)	--	9.4 (39)	9.7 (44)	8.0 (18)

*US = Upstream, DS = Downstream

APPENDIX 3. DISTRIBUTION OF BIRD SPECIES WITHIN GEOMORPHIC REACHES OF THE YELLOWSTONE RIVER

Appendix 3. Occurrence of 64 riparian breeding bird species within geomorphic reaches of the Yellowstone River in 2006 and 2007. Reaches represent segments of the river with distinct geomorphic characteristics. Reaches are ordered by spatial location, with reach A7 being the western-most reach, and D12 the eastern-most (i.e. nearest to the mouth of the river). An 'X' denotes that a species was observed in a particular reach in either or both of the two years of the study.

	Geomorphic Reach																				
Species	A7	A11	A12	A14	A16	A17	A18	B1	B2	B3	B5	B6	B7	B8	C3	C7	C9	D5	D10	D11	D12
American Crow	X	X		X	X	X				X			X	X	X	X		X		X	X
American Goldfinch	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
American Redstart	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
American Robin	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Baltimore Oriole		X		X	X								X				X		X	X	X
Barn Swallow	X							X		X				X		X	X				
Black-and-white Warbler						X		X								X	X		X	X	X
Black-billed Cuckoo								X													X
Black-billed Magpie		X		X	X	X	X	X	X	X			X	X		X	X		X	X	X
Black-capped Chickadee	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Black-headed Grosbeak	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Blue Jay		X								X						X	X		X	X	
Bobolink	X	X				X										X	X				X
Brewers Blackbird		X		X				X									X		X	X	X
Brown Thrasher		X				X		X	X					X	X	X	X		X	X	X
Brown-headed Cowbird	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bullock's Oriole	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X	X		X	X
Cedar Waxwing	X	X	X	X	X	X	X	X		X	X		X		X	X	X	X	X	X	X
Chimney Swift	X					X									X	X	X			X	X
Chipping Sparrow	X			X									X								X
Clay-colored Sparrow		X			X								X			X	X	X	X	X	X
Cliff Swallow	X																				
Common Grackle	X	X	X	X		X		X	X	X	X	X		X		X	X	X	X	X	X
Common Yellowthroat	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Dickcissel	X		X										X				X		X	X	X
Downy Woodpecker	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Eastern Kingbird	X	X		X	X		X	X	X		X			X	X	X	X	X	X	X	X
European Starling	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Field Sparrow					X			X	X	X		X		X		X	X	X	X	X	X
Grasshopper Sparrow																X	X		X	X	X
Gray Catbird	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X		X	X	X
Hairy Woodpecker	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X		X	X	X

Appendix 3 continued.

Species	Geomorphic Reach																				
	A7	A11	A12	A14	A16	A17	A18	B1	B2	B3	B5	B6	B7	B8	C3	C7	C9	D5	D10	D11	D12
House Wren	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lark Sparrow	X	X									X			X		X	X	X		X	X
Lazuli Bunting	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Least Flycatcher	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Mountain Bluebird	X	X																			
Mourning Dove	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Northern Flicker	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Orchard Oriole																X	X				X
Ovenbird	X	X				X		X	X		X				X	X	X		X	X	X
Plumbeous Vireo								X	X	X	X			X	X	X		X	X	X	X
Red-eyed Vireo			X		X	X		X	X	X	X		X	X	X	X	X	X	X	X	X
Red-headed Woodpecker													X	X	X	X	X	X	X	X	X
Red-naped Sapsucker		X																			
Red-winged Blackbird	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X
Rose-breasted Grosbeak																				X	
Savannah Sparrow	X	X						X		X				X	X	X				X	X
Song Sparrow	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X
Spotted Towhee	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Swainson's Thrush	X		X	X				X				X					X				
Tree Swallow	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Vesper Sparrow		X	X					X							X		X				
Violet-green Swallow	X	X		X				X		X				X	X	X					
Warbling Vireo	X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	X	X
Western Kingbird					X	X				X						X	X	X	X	X	
Western Meadowlark	X	X				X	X				X		X	X	X	X	X	X	X	X	X
Western Wood-pewee	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X
White-breasted Nuthatch		X		X	X					X	X			X		X	X		X	X	X
White-throated Swift				X						X					X		X				
Yellow Warbler	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Yellow-bellied Sapsucker																				X	
Yellow-breasted Chat	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Yellow-headed Blackbird	X	X																			

APPENDIX 4. SUMMARY OF RELATIONSHIPS BETWEEN RIPARIAN BIRD COMMUNITY CHARACTERISTICS AND ENVIRONMENTAL VARIABLES

Appendix 4. Summary of general relationships between all response variables representing bird community characteristics and environmental variables. Response variables include: total species richness, Neotropical migrant (NTM) species richness, richness of four foraging guilds, richness of four nesting guilds, and abundance or occupancy of fourteen species. Only statistically significant relationships are reported. For the categorical habitat variable, a relationship is reported if 95% confidence intervals do not overlap between habitat types. For the continuous environmental variables, relationships are reported if the 95% confidence interval for the slope of the relationship does not include zero. A '+' denotes a positive relationship with the variable, and a '–' denotes a negative relationship. When preceded by '~', the relationship is significant at the 90% confidence level. If a cell is empty, then no significant relationship was observed. If a cell is filled with 'NA', then analyses were not conducted for that response variable and environmental variable.

	Cottonwood Habitat Type					Forest Cover	Distance to Settlement	Distance to Crop	River Kilometer
Response Variable	DC. OPENRO	MC. OPENSH	MC. DENSH	MC. LOWSH	OC. GRASS				
Total Species Richness		+	+	–	–	NA	NA	NA	+
NTM Species Richness	+	+	+	–	–	NA	NA	NA	+
Foraging Guild Richness[1]									
FGND	–	+	+		–	NA	NA	NA	NA
FLOW	–	+	+	–	–	NA	NA	NA	NA
FCAN	+ +	+	+	–	– –	NA	NA	NA	NA
FAIR	+			–		NA	NA	NA	NA
Nesting Guild Richness[2]									
NGND	–	~+	+	+	–	NA	NA	NA	NA
NCAV						NA	NA	NA	NA
NLOW	+	+	+	–	–	NA	NA	NA	NA
NMSC						NA	NA	NA	NA
Species Abundance or Occupancy									
Brown-headed Cowbird	NA	NA	NA	NA	NA	–	–		+
Common Yellowthroat						–			–
European Starling		~ +	+	–					+
Gray Catbird	–	~ +	+	–	–	–			+
House Wren	+	–	~ –	~ –	~ –	+			+
Least Flycatcher	+	~ –	–	–	–	+		–	+

[1] Foraging guilds, by location of foraging activity: FGND = ground, FLOW = ground or shrubs, FCAN = shrubs or canopy, FAIR = on the wing
[2] Nesting guilds, by location of nest: NGND = on/close to ground, NCAV = in cavities, NLOW = shrubs or low canopy, NMSC = midstory or high canopy

Response Variable	Cottonwood Habitat Type DC. OPENRO	MC. OPENSH	MC. DENSH	MC. LOWSH	OC. GRASS	Forest Cover	Distance to Settlement	Distance to Crop	River Kilometer
Ovenbird						+			–
Red-eyed Vireo	~ +	–	–	+	–				–
Song Sparrow	–	+	+	–		–			
Spotted Towhee									–
Warbling Vireo	+	–			–	+	+		
Western Wood-pewee						+		–	+
Yellow Warbler	+	+	+	–	~ –	+		–	+
Yellow-breasted Chat	–		+	–	–		–		–

[1] Foraging guilds, by location of foraging activity: FGND = ground, FLOW = ground or shrubs, FCAN = shrubs or canopy, FAIR = on the wing
[2] Nesting guilds, by location of nest: NGND = on/close to ground, NCAV = in cavities, NLOW = shrubs or low canopy, NMSC = midstory or high canopy